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THE BREEDING BIOLOGY OF THE PACIFIC EIDER (*SOMATERIA MOLLISSIMA V-NIGRA* BONAPARTE) ON A BARRIER ISLAND IN THE BEAUFORT SEA, ALASKA

A

THESIS

Presented to the Faculty of the

University of Alaska in partial fulfillment

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for the Degree of

MASTER OF SCIENCE

By

Douglas L. Schamel, B.S.

Fairbanks, Alaska

May, 1974

THE BREEDING BIOLOGY OF THE PACIFIC EIDER (SOMATERIA MOLLISSIMA V-NIGRA BONAPARTE) ON A BARRIER ISLAND IN THE BEAUFORT SEA, ALASKA

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ABSTRACT

The breeding biology of the Pacific Eider (Somateria mollissima v-nigra) was studied on a Beaufort Sea island during 1971 and 1972. Eiders have apparently developed a successful system to avoid both mammalian and avian predation. Eiders did not nest until the island was ice-free, thus avoiding fox predation. By nesting within the territory of resident gulls, at sites complementing their cryptic coloration, eiders received protection from avian predators. The incubation of incomplete clutches may be a special adaptation to shorten the critical stage of nest vulnerability. Seasonal differences in site selection, clutch size, and incubation duration may reflect different year-class birds. Pacific Eiders in this area nested in lower densities than other subspecies of Common Eiders. Although only 33% of the nesting attempts were successful in 1972, 56% of all eggs hatched. King Eiders were almost entirely excluded from potential nest sites by the aggression of the larger Pacific Eiders.

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Many others have assisted with various parts of this study, including Drs. Erk Reimnitz and Peter Barnes, U. S. Geological Survey; Angus Gavin, Environmental Biologist, ARCO; Robert Bartels, graduate student at Iowa State University; Joseph A. Dygas, graduate student at the University of Alaska; and Carl A. Strang, graduate student at Purdue University.

Finally, I would like to thank Diane M. Tracy for her encouragement and critical comments during the assemblage of the thesis.

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INTRODUCTION

Five subspecies of the Common Eider (Somateria mollissima) are currently recognized; four of these occur in North America (A.O.U. 1957). Only two of the subspecies have been studied intensively: the European Eider (S. m. mollissima) (Ahlen and Andersson 1970; Milne 1963) and the American Eider (S. m. dresseri) (Choate 1966; Guignion 1967). A third subspecies, the Northern Eider (S. m. borealis), has been recently investigated for its economic possibilities (Cooch 1965). Only scattered notes on the biology of the Hudson's Bay Eider (S. m. sedentaria) and the Pacific Eider (S. m. v-nigra) exist.

General biological observations of the Pacific Eider have been reported by various researchers, naturalists, and explorers (Anderson 1913; Bailey 1948; Bailey et al. 1933; Dixon 1943; Gabrielson and Lincoln 1959; Grinnell 1900; Kumlien 1879; Leffingwell 1919; Nelson 1887; Turner 1886). Their mating behavior has been studied in detail by McKinney (1961). The general breeding range of this subspecies has been delineated by Gabrielson and Lincoln (1959), with extremes noted by Hibben (1942) and Parmelee et al. (1967). Migration routes and dates have been recorded by Bailey (1948), Conover (1926), Stefansson (1913) and many others. The migration of Pacific Eiders has been studied most

intensively at Barrow, Alaska (Johnson 1971; Thompson and Person 1963), as they and the more numerous King Eiders (Somateria spectabilis) return from breeding grounds along the eastern Beaufort Sea coast. Johnson (1971) also commented on the importance of these ducks to natives, as did Barry (1968). The boundaries of the wintering grounds in the Bering Sea have been roughly outlined, relying upon scattered observations (Bent 1962b; Gabrielson and Lincoln 1959; Kenyon 1961; Kenyon and Brooks 1960).

Although the Pacific Eider has been found to nest inshore in other regions of Alaska (Gabrielson and Lincoln 1959), along the Beaufort Sea coast it is apparently limited to barrier islands. Populations of island-nesting waterfowl are fairly common and generally represent greater nesting concentrations than nearby mainland areas (Hammond and Mann 1956). The establishment of such colonies is thought to be a result of the absence of mammalian predators on the islands (Hammond and Mann 1956; Larson 1960; Barry 1968). However, these waterfowl may be exposed to resident and wandering avian predators (Vermeer 1970; Bourget 1973). The ecological implications of waterfowl-gull nesting associations are seemingly variable (Dwernychuk and Boag 1972; Bourget 1973) and need more study. In such situations, it is of interest to examine the adaptions of both predator and prey species which enable them to coexist as viable populations. Adaptations to avoid nest destruction would be expected to be well developed in the waterfowl. The selection of the nest site, the intraspecific interactions during the selection of these sites, the behavior of the incubating female, and the waterfowl-gull interactions at nest sites may all be important considerations in the ultimate fate of a

nesting attempt. Coincidently, gulls would be expected to have developed adaptations to aid in the location and predation of nests. In addition, if interspecific competition for nest sites occurs, it should result in a divergence of specific nesting chronologies, a differentiation of nest site criteria, or the exclusion of all but one of the competing species. This is extremely important in the arctic, where the breeding season is greatly abbreviated. The present study investigates the interrelationships and adaptations of eiders and gulls in a mixed colony, with emphasis on the breeding biology of the Pacific Eider. With impending offshore oil drilling along the Beaufort Sea coast, there is an urgent need to understand the basic biology of avifauna in this area.

STUDY AREA

Egg Island, Alaska, is a barrier islet located at 70° 26' N and 148° 43' W, on the Beaufort Sea coast (Fig. 1). It lies 8 km northwest of Prudhoe Bay and 4 km northeast of the Kuparuk River delta, an area mentioned by Anderson (1913) as supporting large colonies of breeding eiders on sandspits. During a preliminary survey of islands in this area in July 1971 Egg Island was found to have the greatest concentration of nesting eiders.

The island is relatively small (7.5 ha) and flat (maximum elevation 1.7 m) (Fig. 2) and is comprised of sand and gravel. Vegetation is extremely sparse, both in species and coverage. Only four species were found: Honckenya peploides (Sandbeach Sandwort), Mertensia maritima (Oysterleaf), Elymus arenarius mollis (Lyme Grass), and Puccinellia phryganodes (Alkali Grass) (Fig. 3). Overflow water from the break-up of the Kuparuk inundates low areas of the island, creating temporary ponds. These are utilized for loafing, bathing, and drinking by eiders and other birds until July, when the ponds disappear.

During the winter and early spring, the island is icebound. After spring break-up the north shore becomes susceptible to the action of waves and ice. The extreme instability of Egg Island was first noted by

Figure 1. Map of the central Beaufort Sea coast of Alaska, showing the location of the study area. The eastern tip of the Kuparuk River delta is barely visible southwest of Egg Island.

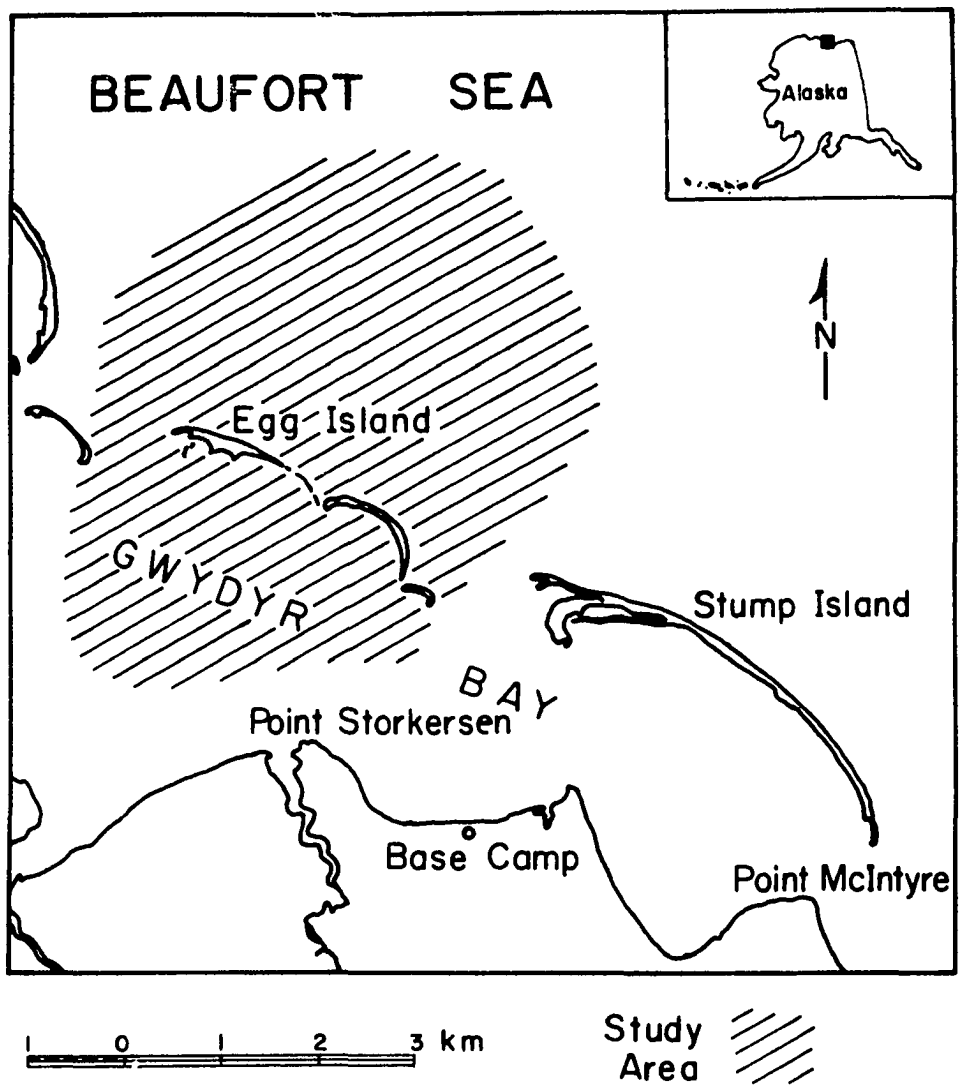


Figure 2. Egg Island, Alaska, showing topography. Contour interval is shown in centimeters above mean high tide.

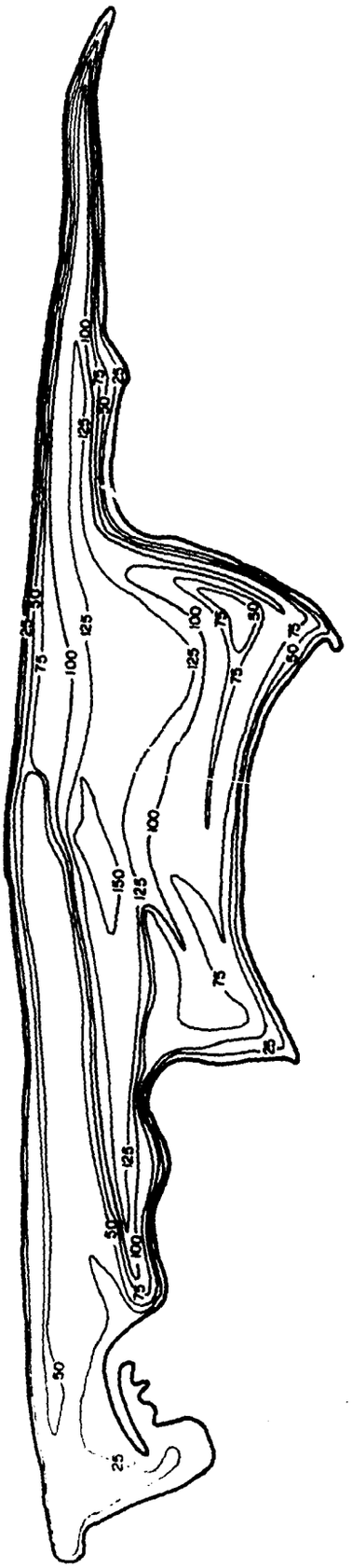
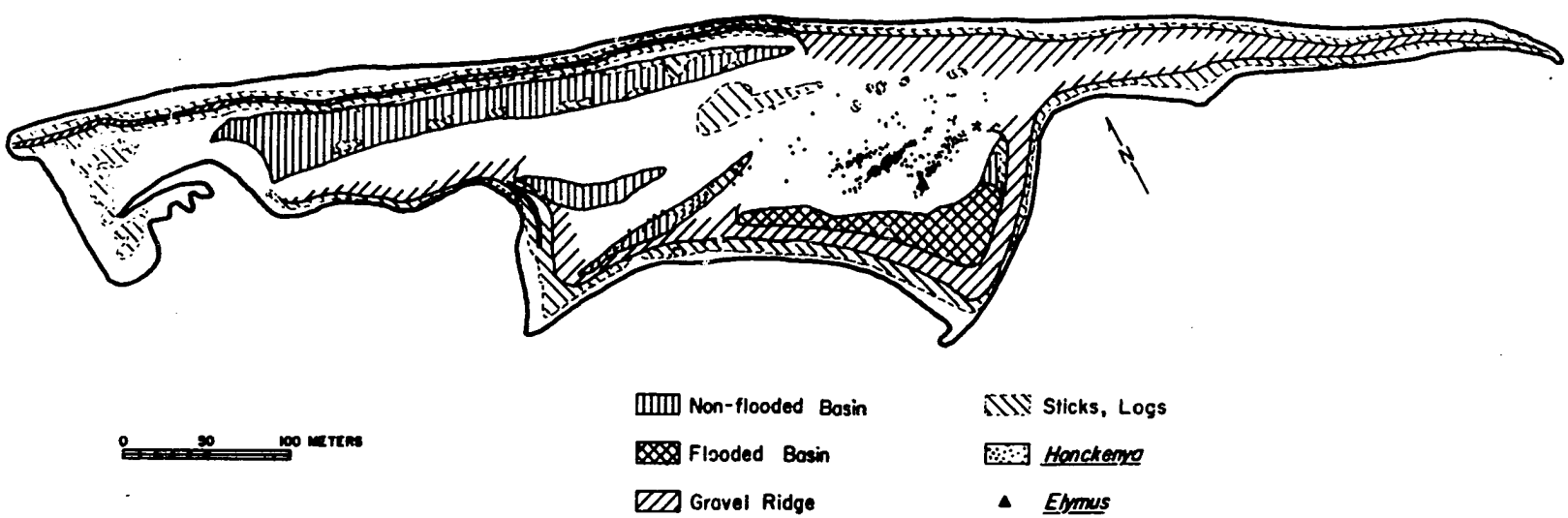


Figure 3. Egg Island, Alaska, showing major habitat features.



Leffingwell (1919). Erosion washed away his beacon in less than 3 years. Two half-buried oil drums indicate that major changes are still occurring. Although tide fluctuations for this area average 15 cm, changes in wind direction and velocity can cause noticeable variations in water level. The influences of wind, ice, and currents constantly rework the island during summer and fall. These probably have the greatest long-range impact on the size and shape of the barrier islands. Fall storms are capable of effecting very rapid and short-term changes (Hume and Schalk 1967). As storm waters recede, scattered sticks and logs are left behind. This material, important to nesting eiders, is deposited at a higher elevation than the high tide mark of late spring and summer, when storms are rare.

Glaucous Gulls (Larus hyperboreus), Arctic Terns (Sterna paradisaea), Black Brant (Branta nigricans), and King Eiders also nested on Egg Island.

METHODS

Information on the Egg Island breeding colony was obtained for the summers of 1971, 1972, and 1973. Data from 1973 were supplied by R. Bergman (personal communication), who visited the island twice during the nesting period. Only during the 1972 field season (20 May through 12 August) was I able to follow the entire nesting process from nest site selection to the departure of the broods. Hence, most of my behavioral observations of these waterfowl rely upon data from a single summer. In 1971 (7 July through 12 August) I did not arrive on the study area until after incubation was well under way.

During both of my summers on Egg Island observations were made using a 20X spotting scope and 7X binoculars and were recorded in field notebooks. A small tent was utilized as a blind during the first summer and was totally unsatisfactory. To minimize disturbances to the birds, it was located 125 m northeast of the Elymus, the center of the colony. At this distance, observations were frequently hampered by dense fog and heat waves. Activity within the blind (cooking, movement, etc.) immediately disrupted the activity patterns of the birds. The temporary nature of the blind also necessitated frequent trips to the mainland base camp.

These difficulties were mitigated in 1972 with the establishment of a wanigan on the island prior to the spring eider migration. It was located less than 30 m north of the center of the 1971 colony. Because we were concerned that human presence might inhibit eider nesting attempts, we minimized our exposure outside the shelter. Eiders did nest on the island, one within 10 m of the shack. Behavioral observations were made on rotating 8-hour shifts, as follows: 0800-1600, 0000-0800, and 1600-2400. Usually an observation week consisted of six days. During the first five days, six 8-hour shifts were covered. The sixth day was devoted to general observations. The two observers watched separate areas. This permitted fairly complete coverage of the avian activities on the island. Weather permitting, we disrupted the regular schedule at least 1 hour each week to record the numbers and activities of all birds on the island and its surrounding waters. This information will appear in a separate report. During the hatching period we utilized a 24-hour observation schedule, sacrificing complete island coverage to maximize pre- and post-hatching information on females and their young. In 1972, clutch size information was estimated for all nests except one by counting the number of young leaving the nest, plus the number of eggs remaining in the nest, plus known predation before hatching. In 1971, clutch size was determined by direct counts during incubation. A nest was considered successful if at least one egg hatched.

Eider activities were recorded to the nearest minute. Only activities at depressions were recorded. (In this paper, "nests" will denote sites at which eggs were deposited and "scrapes" will refer to nest forms

in which no eggs were laid. "Depressions" will be the collective term used to refer to both "nests" and "scrapes.") By so limiting our observations, it was hoped that we would obtain an overall impression of nesting intensity and social tendencies in the colony. Whenever possible, a single pair of eiders was followed. This provided data on movements during nest site selection.

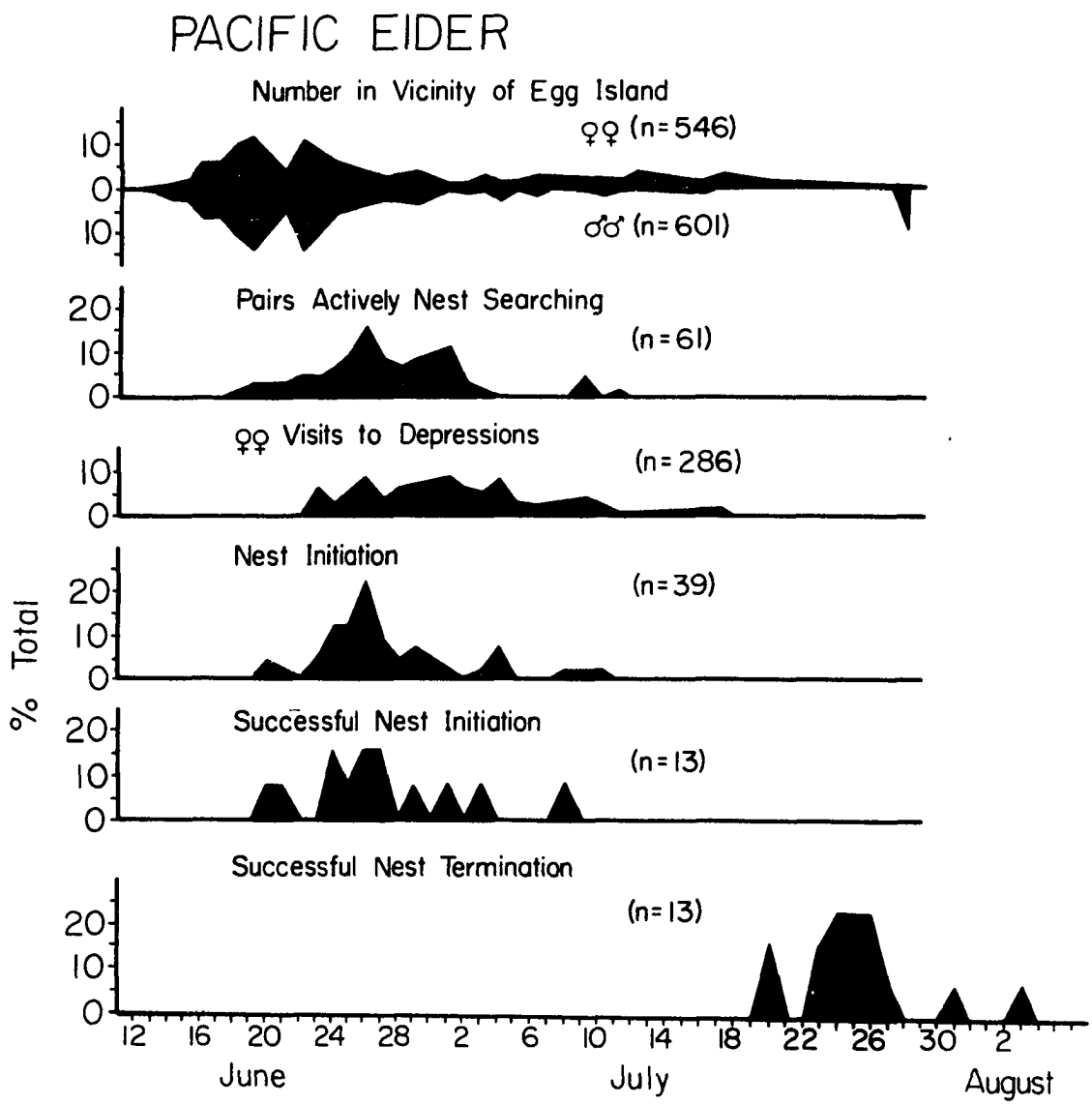
RESULTS AND DISCUSSION

Arrival

The single most important factor in determining the eastward progress of migrating Pacific Eiders is apparently the availability of open water. At Wales, Alaska, Bailey (1948) noted that their first appearance is coincident with the development of open leads. In the present study, the nearby Kuparuk River began to overflow on 1 June 1972 and the first pair of Pacific Eiders was observed the following day. By 4 June there were large flocks of King and Pacific eiders migrating eastward approximately 1.5 km north of the island. Two days later, a few pairs were observed swimming both north and south of the island. The overflow in the Gwydyr Bay and Beaufort Sea was draining through "strudel" holes in the ice by 6 June. Until 10 June, this gradual loss of water had no visible effect on the numbers of eiders utilizing the area. From 10 until 14 June numbers decreased steadily, as did the amount of available water. On 14 June, a large lead was cut to the west of Egg Island by the main channel of the Kuparuk. Numbers of Pacific Eiders in the study area (Fig. 1) then rose dramatically, peaking on 19 and 22 June and declining to a stable number by 1 July (Fig. 4).

The main route followed by the migrating eiders appeared to coincide with the northernmost edge of the extension of overflow into the Beaufort Sea. A few flocks followed the barrier islands and the coast-

Figure 4. Chronology of main events of the Pacific Eider during the spring and summer of 1972.



line, both of which were at least partially free of snow. These latter two routes were heavily used by those waterfowl which arrived prior to break-up. Anderson (1937) noted that the Pacific Eiders in northwestern Canada follow narrow, regular migration routes: open leads in early spring and exposed earth banks along the coast in late spring.

The importance of the timing of break-up to the arrival of other subspecies of Common Eider has been indicated by several researchers. Cooch (1965) found that the first Northern Eiders arrived 2 days after the thaw of inland lakes in 1955 and 3 days post-thaw in 1956. In his study of Hudson's Bay Eiders, Freeman (1970) reported that the first birds were observed within 24 hours of the beginning of break-up.

Little, if any, courtship activity was seen near Egg Island. It is possible that pairing had already occurred by the time of their arrival. This thought was also expressed by Dement'ev et al. (1967) and Nelson (1887) for the Pacific Eider, Guignion (1967) for the American Eider and Freeman (1970) for the Hudson's Bay Eider. On Amchitka Island, Kenyon (1961) recorded Pacific Eiders pairing in early May and a mating in late June.

Although Pacific Eiders had been seen in the vicinity of Egg Island since 2 June, none were noted on the island until the ice sheet connecting it to the mainland was broken. On 16 June, the southwest end of the island was ice-free. By 20 June, the entire south shore of the island was separated from the ice sheet by 5 m of open water. The first pair of Pacific Eiders seen on the island was observed at 0300 on 18 June.

Nest Searching

Pacific Eider pairs were actively nest searching from their arrival on Egg Island until 11 July (Fig. 4). Nest searching involves the movement of pairs or females from one potential nest site to another. Each site is investigated by the eiders. I have divided potential nest sites into two basic types: depressions remaining from the previous season and suitable habitats lacking such depressions. The former are referred to as old sites or depressions; a depression constructed at the latter is considered to be new. The significance of this division will be discussed as part of the site selection criteria. Female eiders investigate potential nest sites by probing the materials at the site with their bills. If the site is not acceptable, they continue their search. If it is acceptable, the female eider then sits and scratches, alternating feet and shifting body position so that all materials are pushed out behind the bird (Milne 1963). When investigating old nests, they are able to rid the site of old materials by rotating during this process.

During the early stages of nest searching and investigating, frequent intraspecific encounters occur. These consist of aggressive displays and physical combat. Both members of the pair take part in these encounters. Vocalizations form a conspicuous component of the aggressive displays. Males have ritualized much of their vocalizations into "cooing movements," similar to those described for courtship by McKinney (1961). Females give "gog-gog" calls (McKinney 1961), often accompanied by inciting. Males seldom make physical contact. Their agonism is generally restricted to vocalizations and bluff charges. However, if a female intensively incites her mate, he may attack another male or, more rarely,

another female. The attack consists of biting and "push-pulling" the antagonist. "Push-pulling" is accomplished by successive head thrusts while clasping the opponent with the bill. The more common regions bitten are the tail, back, and neck. Females readily make physical contact during aggressive encounters. Their attacks are generally more intense and of longer duration than those of males. During extremely intense inciting a female often attacks her own mate repeatedly, ceasing only after he either flees the area or attacks the intruding pair. It is important to note that the outcome of the female-female encounters, not the male-male, determines the possession of a potential nest site.

Retention of depressions by females was most readily achieved by "sitting tight." This behavior is merely a refusal of the female to move from the site she occupies. Those birds which "sit tight" during intraspecific encounters never lose possession of a depression to a nest searching bird. "Sitting tight" is sometimes coupled with defensive biting, which quickly discourages attackers. The successful defense of a potential nest site does not automatically imply that the victor will remain there. An aggressive female frequently drives a less dominant female from several successive depressions, then departs from the island. "Sitting tight" was most commonly, though not exclusively, noted in laying birds. Their tenacity to a nest site increased noticeably with the deposition of the first egg.

In a few instances, I was able to follow the movements of nest searching pairs for several hours. Eiders revisited the same nest occupied by another bird several times. Their nest searching efforts appeared to radiate from this site. As more nests are initiated and incubated,

there are more potential centers of nest-searching activity. However, I found that the first nests to be incubated are the main centers of activity throughout the season.

Males on the Breeding Grounds

Although the amount of time spent by male Common Eiders on the breeding grounds is variable among and within the subspecies, all sources agree that their role in nest site selection and defense is minimal. Gross (1938) reported that the pair bond terminates after courtship in the American Eider and the male never approaches the nest. In sharp contrast, Gudmundsson (1932) found the male European Eider to remain with its mate until the end of the incubation period. In the present study, early-nesting birds maintained their pair bond through the first few days of incubation, while late-nesting birds terminated theirs prior to or during nest initiation.

During nest searching, the male accompanies the female to the potential nest sites, usually following. Occasionally, males were observed investigating an old scrape while their females were searching or investigating nearby. On rare occasions, males led females across the island towards a potential nest site. In all such cases, the females stopped to investigate another site before the male reached his objective. At least two males remained close to their mates for 5 days after nest initiation. These were the two earliest nesting pairs. One of these males actively defended a pond near the nest until his departure from the island. His territory also included the nest of his mate and a small corridor between it and the pond. Agonistic behavior by this male was noted towards

conspecifics and towards King Eiders, Oldsquaws (Clangula hyemalis), Arctic Terns, and Glaucous Gulls. The most intense aggression was exhibited on the pond and lesser amounts were seen away from the pond and near the nest. With the beginning of incubation, male defense of the territory seemed to diminish rapidly in frequency and intensity and was soon limited to the pond. The amount of time spent defending the pond also decreased daily. This is the first reported observation of territoriality in the male Pacific Eider on the breeding grounds.

Summer Migration

In 1972, the westward migration of male Pacific Eiders is thought to have begun no later than 4 July. The mates of the earliest nesting females had departed from the island by 26 June. It is not known how long they remained in the area before migrating. By 4 July, most of the males had ceased nest searching activities with their mates, although a few were active until 11 July (Fig. 4). Thus, they were free to head westward to the wintering grounds. Anderson (1913, 1937) stated that the males move westward as soon as the eggs are laid. At Humphrey Point, east of Prudhoe Bay, Dixon (1943) noted flocks of males flying west on 5 July 1912. The 1972 migration was not well under way until 11 July, however, and seemed to reach peak numbers towards the end of July. This generally agrees with the data of Johnson (1971) at Barrow, Alaska in 1970.

Nest Site Selection

Physical Aspects

In Alaska, Pacific Eiders nest on both the coastal tundra and

offshore islands. Their nests are placed under overhanging rocks, under low bushes, on gravel beaches, and in depressions sheltered by short grasses (Gabrielson and Lincoln 1959). In the Prudhoe Bay area, these birds nest exclusively on offshore islands. Other subspecies of the Common Eider have also been noted as regular breeders on islands that are flat, low and either sparsely vegetated or covered with short grasses (Ahlen and Andersson 1970; Choate 1966; Gudmundsson 1932; Hilden 1964). The establishment of these offshore breeding islands has been attributed to the predatory activity of the Arctic Fox (Alopex lagopus) inland (Ahlen and Andersson 1970; Errington 1961; Larson 1960; Lewis 1942). Barry (1968) suggests that all waterfowl smaller than the Black Brant are incapable of successfully defending their nests from this predator. These birds are thus forced to utilize breeding areas inaccessible to foxes. The fact that no eiders were seen on Egg Island until the ice link with the mainland was completely broken lends additional credence to Barry's statement. Nest predation by Arctic Foxes in the vicinity of the base camp (Fig. 1) was significant during the years of this study (R. Bergman, personal communication). Denning foxes were observed in the Point McIntyre (R. Bergman, personal communication) and Prudhoe Bay area (Underwood 1974).

Although the Beaufort Sea barrier islands are quite barren, they provide a variety of habitats for nesting waterfowl (Figs. 2 and 3). They all have a conspicuous line of drift debris on both the north and south shores. Vegetation, though sparse, is frequently present. Gravel ridges contrast in elevation with overflow basins and can provide wind protection for nesting birds.

Despite the apparent little use of Elymus (Table 1), it should be emphasized that only one small clump of this species was located on Egg Island (Table 2). During 1971 and 1972, this was the first site to be occupied by nesting waterfowl. Although the chronology of nest initiation for 1973 is lacking, it is known that this site was occupied (R. Bergman, personal communication). This is the only nest site that was incubated for each of the 3 years. This was also the center of the most intensive and most frequent intraspecific interactions during the nest searching and initiating period, as well as the main center of activity throughout the remainder of the breeding season. I therefore consider it to be the cover type most preferred by eiders. Elymus is the most common nest cover of the Pacific Eider in the Aleutian Islands (C. P. Dau, personal communication). It is also important to nesting Hudson's Bay Eiders (Freeman 1970) and European Eiders (Gudmundsson 1932). In Spitsbergen, a similar grass, Festuca rubra, provides the preferred nest cover type (Ahlen and Andersson 1970). Finding a similarity between the width of Elymus blades and the width of the white flecking in the plumage of female Pacific Eiders, C. P. Dau (personal communication) suggested that these birds are admirably camouflaged when nesting in this grass. Elymus is utilized as part of the base of the nest depression and may provide good insulation for the eggs.

The second most preferred nest cover appears to be Honckenya. Although not utilized for nesting sites in 1972, these plants received heavy use in other years (Table 2). This species occurs in small, scattered clumps (range: 30-1850 cm^2) and is generally found in the vicinity of Elymus (Fig. 3). Honckenya, however, provides neither the

Table 1. Cover types at nests incubated by Pacific and King eiders.

Main Cover Type	Nests 1971 N	1971 %	1972 N	1972 %	1973 N	1973 %	Total N	Total %
Sticks, logs	12	70	9[b]	60[b]	14	60	35	64
Honckenya	4	24	0	0	7	30	11	20
Elymus	0[a]	0[a]	2	13	1	5	3	5
Old gull nest	0	0	3	20	0	0	3	6
None	1	6	1	7	1	5	3	5

[a]Occupied by Black Brant prior to arrival of eiders.

[b]Includes one King Eider nest.

Table 2. Selected habitat types, their abundance and utilization by incubating Pacific and King eiders.

Habitat Type	Coverage (m^2)	Nests per ha 1971	1972	1973
Sticks, gull nests	7,500	18	18[b]	21
Elymus	0.49	0[a]	40800	20400
Honckenya	35	1140	0	1990
Overall[c]	75,000	2.3	2.0	2.9
Overall[d]	75,000		5.4	

[a]Occupied by Black Brant prior to arrival of eiders.

[b]Includes one King Eider and one deserted Pacific Eider nest.

[c]Overall incubated nest densities.

[d]Overall initiated nest densities.

dense cover nor the insulating qualities of the latter, though it may offer similar protective coloration. When in their defensive position (body flattened, neck outstretched and lowered), incubating Pacific Eider females superficially resemble the denser, larger mounds of Honckenya. The plant may thus provide additional camouflage for them. It has been suggested that in the case of the European Eider, vegetation may appear secondarily, following the deposition of guano by nesting birds (Belopol'skiĭ 1961; Dement'ev et al. 1967). Use of the same site in successive years expedites this process. The fact that Common Eiders are strongly tenacious has been established by various banding studies (Choate 1966; Cooch 1965; Milne 1963). Although there is some behavioral evidence that the first nest searching pairs of Pacific Eiders on Egg Island were acquainted with the location of the old nest sites, such evidence is far from conclusive. It is not known whether the vegetation found on this island occurred as a result of the presence of nesting waterfowl or independently of their influence.

Although sticks and logs provide cover for the largest number of nests (Table 1), this cover type seems to be less preferred than those discussed above (Table 2). Because of their abundance, sticks are nevertheless extremely important to the overall production of the Pacific Eider in this area. Sticks can provide both a visual barrier to potential predators and a physical barrier to the wind. Many of the available sticks are located in the drift debris line created by past fall storms. This debris line is generally located at a low elevation and could be potentially flooded during summer storms.

In addition to the type of cover, eiders seem to have a definite preference as to its positioning with respect to the nest, though not with its location on the island. The birds tend to choose sites that afford some protection on the north side (Table 3). This protection is provided by vegetation, sticks, and elevated gravel ridges. It is possible that the eiders are selecting for protection from the prevailing northeast wind, which could blow the down from unattended nests, leaving them exposed to predators. Cooch (1965) suggested that sites along south or southwest facing ridges are snow-free and well-drained (and therefore available for use) early in the season. In the present study, it appeared that these slopes were the last to become free of snow, due to drifting. The fact that equal numbers of nests (19, 20) were initiated on each half of the island in 1972 indicates that the eiders had no definite locational preferences that year. However, a substantially higher proportion of successful nests were located in the south (Table 4). On nearby Stump Island, a significantly higher proportion of nests were located on the south side of the island than on the north in 1972 ($\underline{X}^2 = 4.59$, $0.025 < P < 0.05$). There were similar findings for the distribution of depressions on this island in 1971 ($\underline{X}^2 = 8.79$, $P < 0.005$) and 1972 ($\underline{X}^2 = 15.70$, $P < 0.005$). This compares favorably with Egg Island depressions in 1972 ($\underline{X}^2 = 9.16$, $P < 0.005$) but not with those from 1971 ($\underline{X}^2 = 2.33$, $0.25 < P < 0.1$).

Eiders locate their nests within a wide range of elevations above sea level (Table 5). If wind protection is available, they can nest at a high elevation, but appear to be limited at low elevations, perhaps by the dampness of the site and its close proximity to water. Although the

Table 3. Wind protection at nests incubated by Pacific and King eiders.

Protected Side	Nests 1971 N	1971 %	1972 N	1972 %	1973 N	1973 %	Total N	Total %
North	17	100	14[a]	93[a]	18	78	49	89
South	3	18	9[a]	60[a]	10	44	22	40
East	3	18	11[a]	73[a]	16	70	30	54
West	7	41	9[a]	60[a]	12	52	28	51

[a]Includes one King Eider and one deserted Pacific Eider nest.

Table 4. Geographical location of nests incubated by Pacific and King eiders.

Location on Island	Nests					
	1971		1972		Total	
	N	%	N	%	N	%
North	5	29	5[a]	33[a]	10	31
South	12	71	10[b]	67[b]	22	69

[a]Includes one King Eider nest.

[b]Includes one deserted Pacific Eider nest.

Table 5. Elevation above sea level of Pacific and King eider nests.

Nest Category	N	Elevation (m) $\bar{X}$ ± 95% C.L.	Range
1971 successful	17	1.07 ± 0.13	0.50-1.45
1972 successful[a]	15	0.78 ± 0.20	0.32-1.37
unsuccessful	17	0.70 ± 0.16	0.28-1.37

[a]Includes one deserted Pacific Eider and one successful King Eider nest.

t-test shows new depressions to be located at a significantly lower elevation than old depressions ($P < 0.001$), it is interesting that no significant difference in elevation was found between old and new nests ($0.4 < P < 0.5$) or old and new successful nests ($P > 0.5$). Of the old sites, those at a lower elevation seemed to be preferred ($0.05 < P < 0.1$), while the more elevated of the new sites may be preferred ($0.1 < P < 0.2$). Old sites are utilized significantly earlier than new sites by nesting birds ($0.01 < P < 0.02$). Regression analysis shows that eiders use significantly more elevated nests at the beginning of the season and lower sites later ($0.01 < P < 0.05$). This may be related to the moisture regimes of different elevations over time. In general, the higher elevations become dry early in the season while the lower areas retain their moisture for a longer period. Due to the nature of the study, however, no data were collected which substantiate this observation.

Regression analysis shows the elevation of a depression to correlate strongly with its distance from water ($F = 242.13$, $P < 0.01$) (Fig. 2). Egg Island was small enough that no point was very far from water (maximum distance = 93 m). Behavioral observations on nest-searching pairs and females with broods indicate that this parameter, by itself, is probably not of prime importance in site selection or nest success.

Intraspecific Aspects

Social aspects of the selection of successful sites were also considered. The intraspecific behavior of the Pacific Eider during nest searching and initiating has been discussed under Nest Searching. In an effort to examine these influences on site selection, distances were

measured from recently initiated nests to: (1) the nearest incubated eider nest; (2) the next nearest incubated eider nest; (3) the nearest active, but non-incubated nest; and (4) the next nearest active, non-incubated nest (Table 6). In all cases, no significant differences were found between successful and unsuccessful nests. This suggests that these social factors may not be important in the ultimate success or failure of a nest site.

Interspecific Social Aspects

Interspecific social aspects were examined as well, particularly gull-eider relationships. The fact that gulls and waterfowl often associate in mixed colonies is well established (Bourget 1973). Although Koskimies (1957b) has suggested that nesting larids may form part of the site selection criteria of these waterfowl, such an association may be due simply to a similarity of physical habitat preferences of the species (Evans 1970). In the present study, eiders frequently investigated old gull nests. Eggs were deposited in four of these sites. Three of these nests were incubated, two successfully. The third was deserted. It may have been too close to the field camp (10 m). Dement'ev et al. (1967) reported heavy utilization of gull nests whose eggs had been removed prior to the arrival of eiders. Nest site overlap was also recorded by Guignion (1967), who found several mixed clutches of gull and eider eggs. The adaptive significance of such gull-waterfowl associations is still unclear. Some believe them to be advantageous for the waterfowl (Bourget 1973; Choate 1966) while others claim these associations to be an "ecological trap" (Dwernychuk and Boag 1972:559).

Table 6. Distances (m) from Pacific and King eider nests to incubated and active eider nests in 1972.

Nest Category	N	Nest Fate: Successful[a]	N	Nest Fate: Unsuccessful
Active				
Nearest	14	153.6 ± 62.1[b]	21	97.3 ± 21.4
Next nearest	9	152.1 ± 101.0	20	173.0 ± 53.6
Incubated				
Nearest	13	61.9 ± 35.6	23	73.7 ± 19.8
Next nearest	13	148.0 ± 67.2	23	150.9 ± 25.8

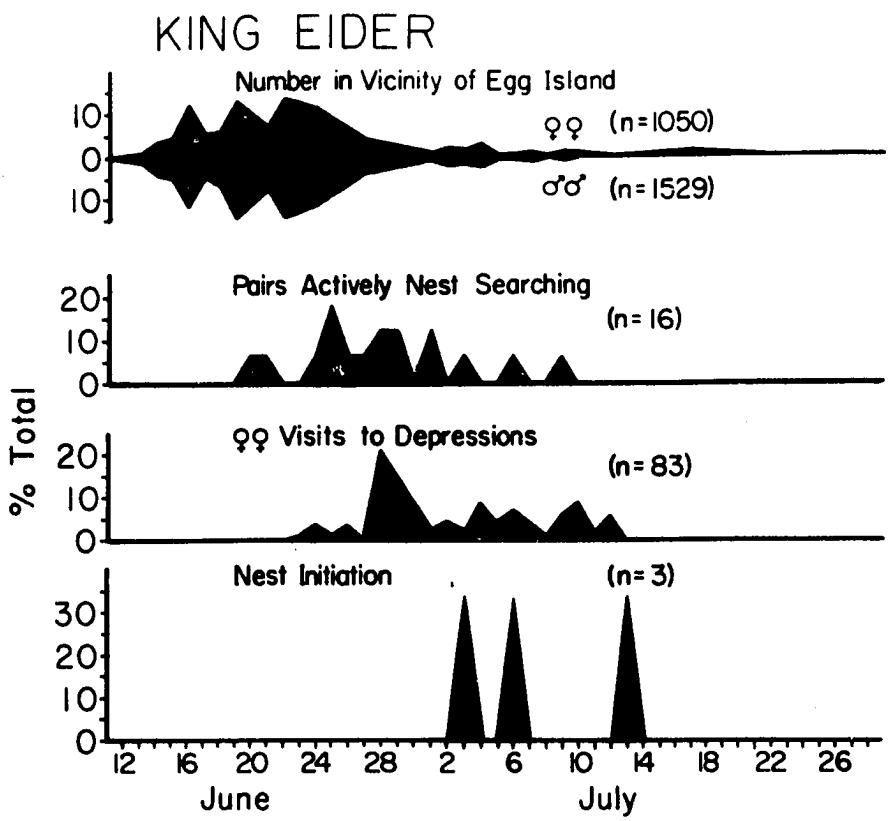
[a]Includes one deserted Pacific Eider nest and one King Eider nest.

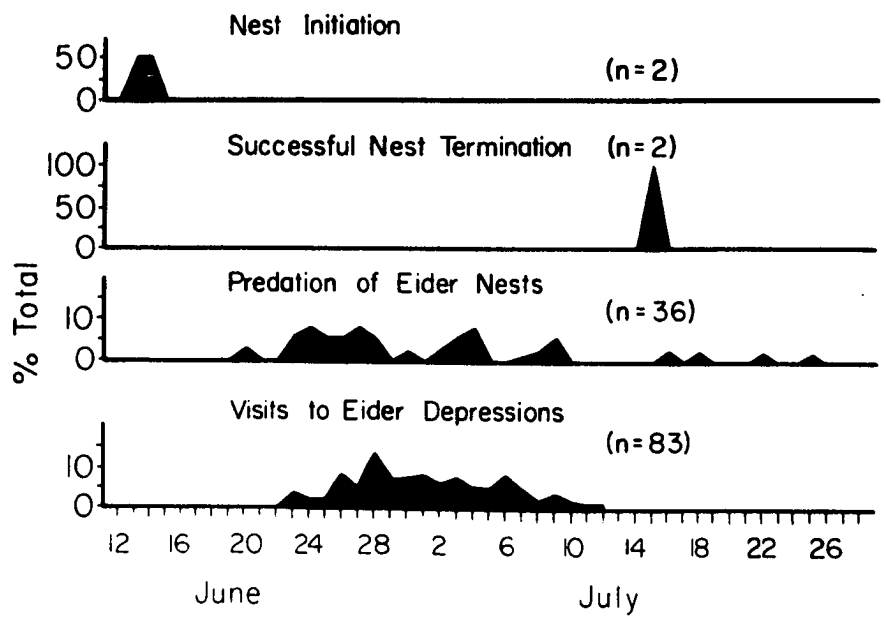
[b]$\bar{X}$ distance (m) ± 95% confidence limits.

Nesting Glaucous Gulls were found on Egg Island all three years (R. Bergman, personal communication). In 1972 gulls were present on the island for the entire field season. Courtship and copulation were first noted shortly after the Kuparuk River began to overflow. Nest initiation occurred on 15 and 16 June. Incubation had begun by 18 June. Hatching was completed by 17 July. Thus, Glaucous Gulls were incubating their nests by the time Pacific Eiders arrived on Egg Island. The gull nests also terminated before eider nests (Fig. 5).

In the present study it was found that successful nests tended to be located nearer to active gull nests than were unsuccessful nests ($0.05 < \underline{P} < 0.1$). Successful nests were 108.4 ± 41.7 m ($\bar{X}$ ± 95% confidence limits) from gull nests; unsuccessful nests were 159.6 ± 34.5 m from gull nests. Of the new depressions, those utilized by eiders also tended to be nearer to active gull nests than those not used ($0.05 < \underline{P} < 0.1$). Examining the distance from a newly-initiated nest to the nearest destroyed nest, it was found that successful sites were significantly nearer ($0.01 < \underline{P} < 0.02$) to gull nests (41.9 ± 23.7 m) than those which were ultimately predated (78.3 ± 31.5 m). In his study of the interrelationships of gulls and American Eiders in Penobscot Bay, Maine, Bourget (1973) suggested that resident gulls may actually reduce the potential predation rate by warding off wandering avian predators. Gulls resident on Egg Island were sometimes observed chasing non-resident gulls, Pomarine Jaegers (Stercorarius pomarinus), Parasitic Jaegers (Stercorarius parasiticus), and Long-tailed Jaegers (Stercorarius longicaudus) from the island. It is possible that the resident gulls thus afford some protection to eiders nesting within their territories. These relationships are

Figure 5. Chronology of main events of the King Eider and Glaucous Gull during the spring and summer of 1972.





summarized in Tables 7 and 8. Note that successful eider nests were located closer to Glaucous Gull nests in 1971 than in 1972. This may be a consequence of fewer gull nests in 1972. It may be related to gull territory size differences between the two years. In 1971, nine pairs of Glaucous Gulls nested on Egg Island, compared to two pairs in 1972. One would suspect the territories to be larger in 1972. Eiders could therefore retain the protection of territorial gulls in 1972 while nesting further from their sites. Choate (1966) suggested that nesting gulls may offer protection to eiders unless the nests of the latter are either too close or too far away. Contrast the sharp increase in destroyed versus successful nests further than 100 m from a gull nest (Table 8). This may be approaching the boundary of the gull's territory. The fact that no successful nests were initiated less than 18 m from a gull nest (Table 7) seems to indicate a critical minimum distance as well.

Similar predator-prey associations have been noted by other researchers. Pacific Eiders in the Aleutians have been found to nest near Peregrine Falcon (Falco peregrinus) nests (Turner 1886). Snow Geese (Chen caerulescens) were found nesting in association with Snowy Owls (Nyctea scandiaca) on Wrangell Island (Minyeev, cited in Portenko 1937).

Predation

Eiders nesting in association with gulls may receive protection from wandering avian predators. However, they also suffer some losses to the resident gulls. It is well known that the Glaucous Gull is a frequent predator of eider eggs and young (Belopol'skiĭ 1961; Freeman 1970; Kumlien 1879; Larson 1960). On Egg Island, all known predation was

Table 7. Mean distance of Pacific and King eider nests from the nearest Glaucous Gull nest.

Nest Category	N	Distance from gull nest (m) $\bar{X}$ ± 95% C.L.	Range
1971 successful	17	79.1 ± 43.6	18.0-308.0
1972 successful[a]	15	108.2 ± 41.9	22.5-268.0
unsuccessful	17	159.6 ± 34.5	10.5-255.0

[a]Includes one deserted Pacific Eider nest and one King Eider nest.

Table 8. Distribution of distances of Pacific and King eider nests from the nearest Glaucous Gull nest.

	Distance from gull nest (m)											
	<50		>50 <100		>100 <150		>150 <200		>200 <300		>300	
	N	%	N	%	N	%	N	%	N	%	N	%
1971												
Incubated nests	12	70	1	6	1	6	1	6	1	6	1	6
1972												
Incubated nests	1	7	9[a]	60	1	7	1	7	3[b]	19[b]	-	-
Non-incubated nests	1	6	3	18	3	18	5	29	5	29	-	-

[a]Includes one deserted Pacific Eider nest.

[b]Includes one King Eider nest.

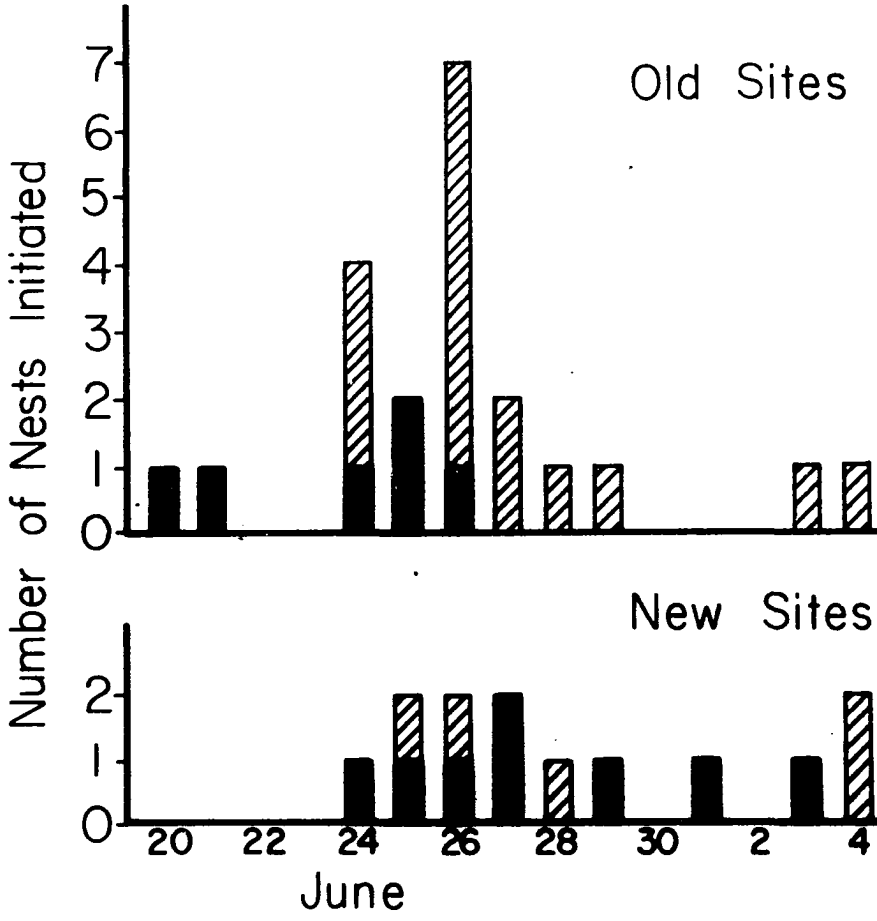
attributed to these gulls, who devoured nearly half the eggs produced by eiders in 1972 (Table 9). Nest predation by Glaucous Gulls follows closely, but not precisely, the pattern of eider nest initiation (Figs. 4 and 5). There is no significant difference between the dates of successful eider nest initiation and those of unsuccessful sites (t = 0.78, $0.4 < P < 0.5$, N = 44). When the dates of initiation and predation of nests at old versus new sites are compared, a difference is noted. Although gull predation at old sites may occur only slightly later than the peak of initiation at these sites (t = 0.77, $0.4 < P < 0.5$, N = 40), successful sites were initiated significantly earlier than predated sites (t = 2.21, $0.025 < P < 0.05$, N = 23). New sites showed the same trends (t = 0.56, $P > 0.5$, N = 23; t = 2.6, $0.01 < P < 0.025$, N = 16). These data suggest that the earliest initiated nests in each of the two nest classes had the best probability of success (Fig. 6).

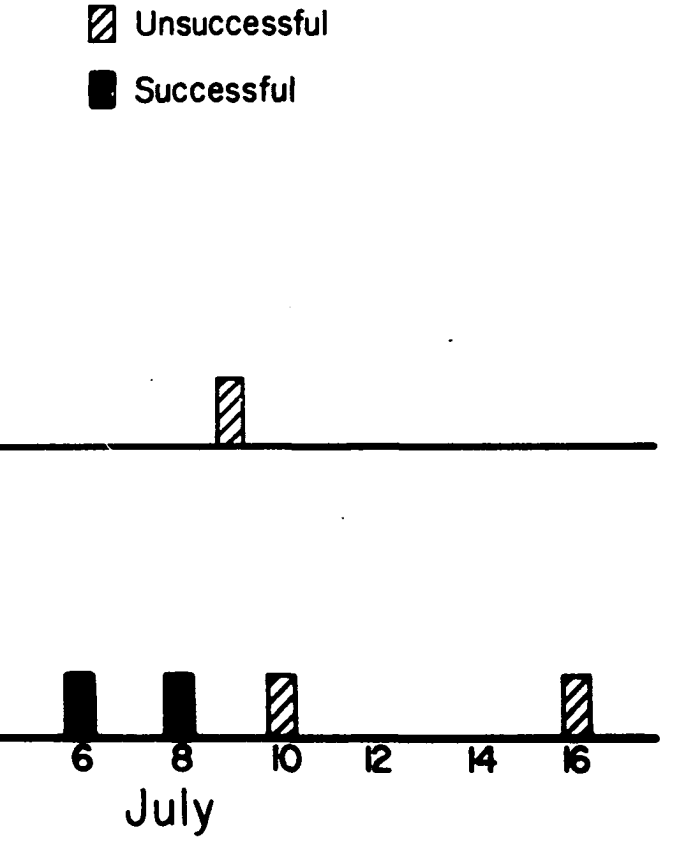
I have previously established that old depressions are utilized earlier in the season and new sites later. This may relate to a behavioral difference between eiders of different year classes or to gull predation. Note from Figure 6 that although nests were initiated at old sites after 26 June, none were successful. Note also the large number of destroyed nests at old sites on this date. There was a sufficient lag period between the beginning of initiation of nests and predation at these sites to allow the early nests to escape destruction. Dates of gull visits to old sites were significantly later than both eider visits (t = 3.11, $0.001 < P < 0.005$, N = 283) and nest initiation (t = 3.75, $P < 0.001$, N = 159). I believe that the gulls learned to hunt for eggs. By 26

Table 9. Fate of Pacific and King eider eggs on Egg Island in 1972.

Fate of Eggs	N	%
Hatched	63	58
Destroyed by gulls	45	42
During absence of female eider in laying stage	32	30
Following desertion	13	12
Gull-induced	2	2
Human disturbance	2	2
During incubation	3	3
Post-nest termination	6	5
Total	108	100

Figure 6. Fate of Pacific and King eider nests initiated at old and new sites on Egg Island in 1972.




Unsuccessful
Successful
6
8
10
12
14
16
July

June, they had become highly successful at locating old sites. At this time, nest initiation had already begun at new sites. Although the early nests were again more successful than later ones, there was no significant time lag between gull visits to these nests and the predation of these sites ($t = 0.072$, $P > 0.5$, $N = 22$) as in the case of the old sites ($t = 2.65$, $0.005 < P < 0.01$, $N = 153$). It seems feasible that the gulls had transferred their learning to the new sites. Finding an increased rate of predation at the end of the nesting season, Milne (1963) suggested that predators may have grown more aware of nesting attempts by the eiders.

Of the nesting attempts at new sites after 26 June, 42% were successful, while none were successful at old sites. This apparent discrepancy may be explained by the different methods of predation associated with old and new sites. Old depressions were predominantly located in the center of the island (Figs. 7 and 8). As eiders began to visit these depressions, so did the gulls. They usually visited these sites while the female eider was present or soon after her departure. In general, the more intense the eider interactions at these sites, the more interested the gull. Gulls were also drawn to females "sitting tight" on a depression. In this manner, the gulls soon learned the location of the more frequently and intensely visited sites. These depressions were routinely examined by gulls on patrol. A patrol consisted of systematic searching while following a relatively regular route. During patrols, gulls predictably visited sites intensively investigated by eiders, often flying from one depression to another, without searching the area between them. More often, the examination of exact sites was coupled with a

Figure 7. Egg Island, Alaska, showing the location of nests and scrapes in 1971.

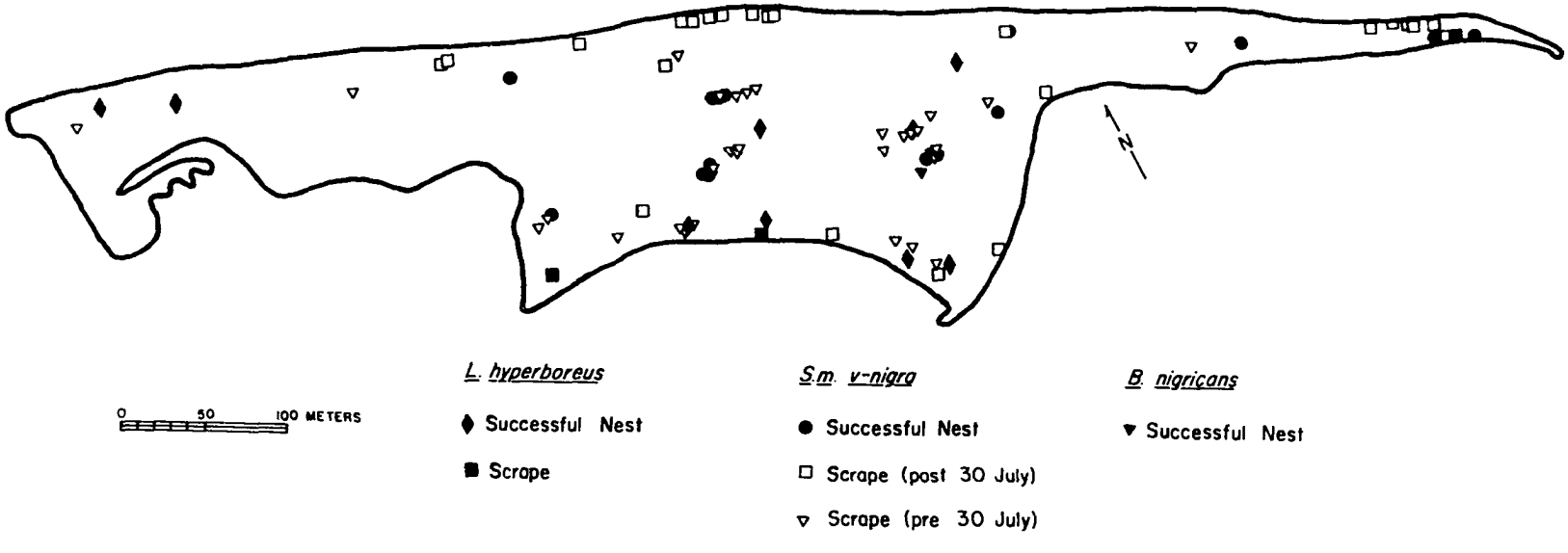
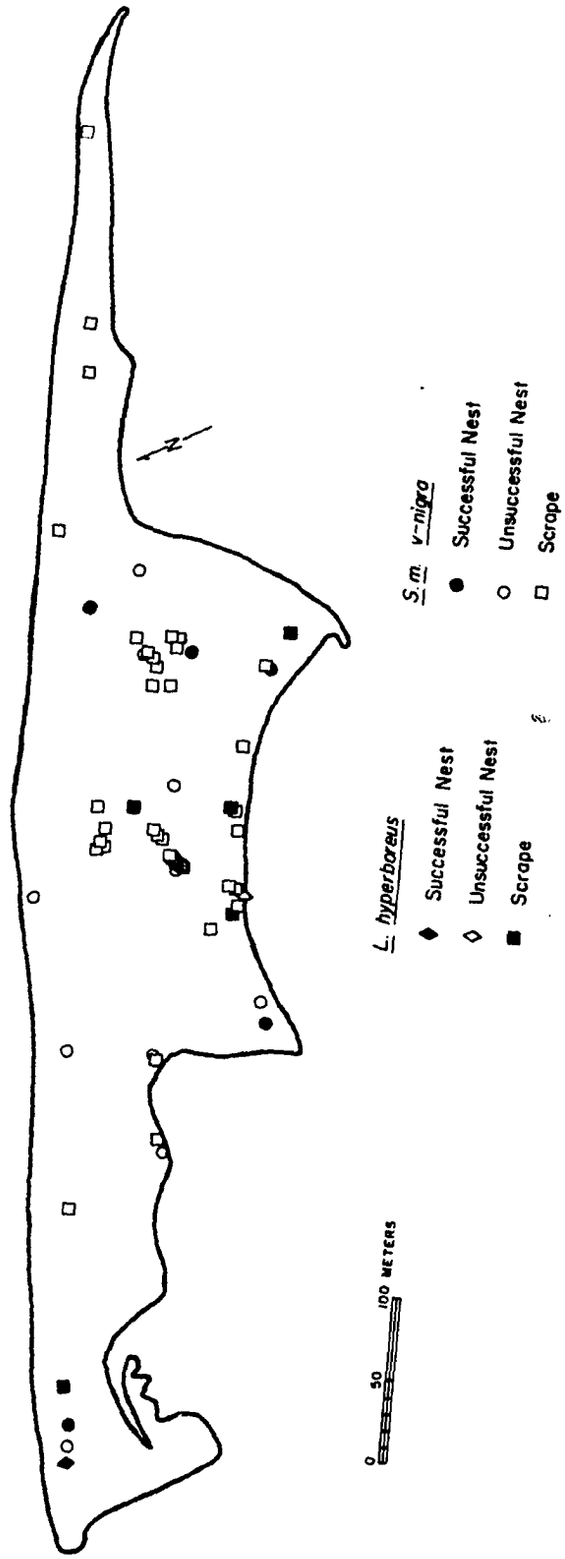


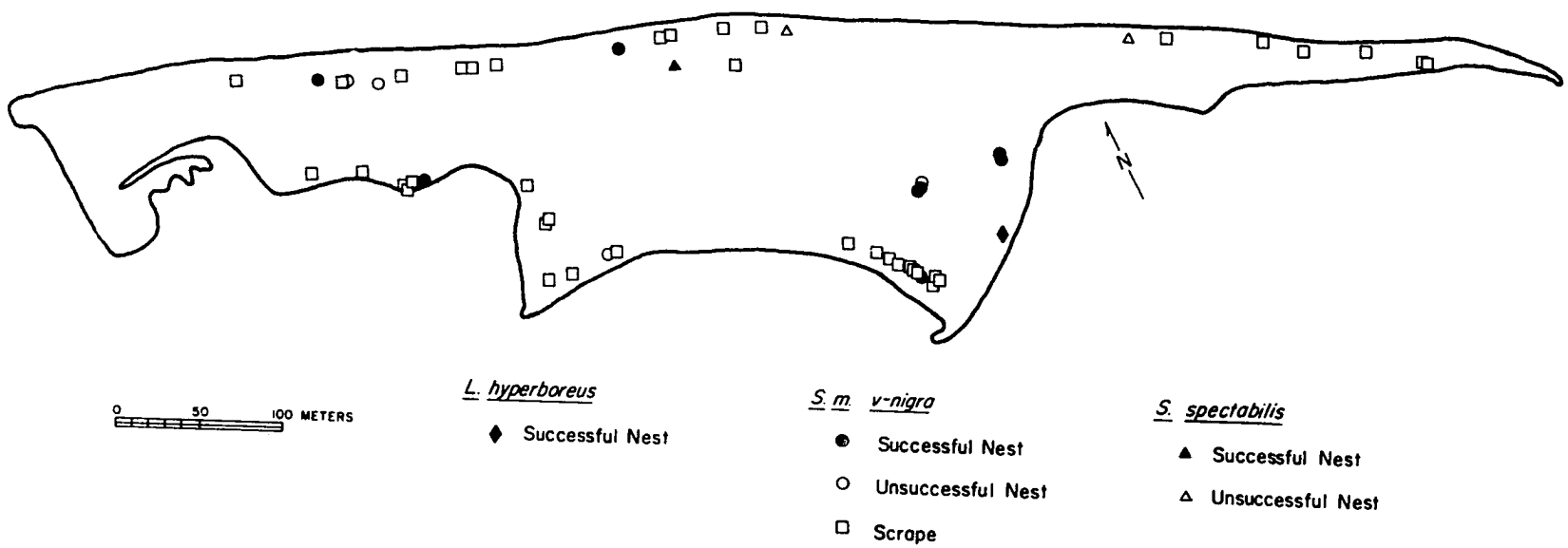
Figure 8. Egg Island, Alaska, showing the location of sites remaining from the 1971 season and describing their utilization in 1972.



general search along the high water drift debris line. Since this was well above the summer debris line, it is unlikely that the gulls were searching for refuse. The only edible objects they found in this area were eggs. Thus, this appeared to be a specialized activity. While walking through the debris, gulls overturned and tossed aside mats of vegetation and small sticks. In this manner, they were able to locate some of the new nest sites, most of which were located in the drift debris (Figs. 7 and 9). When a nest was located, it became one of the routinely visited sites. Unless a depression was continuously occupied or closely tended by an eider before it became part of a gull's regular patrol, it had a very poor probability of success. Only one of six nests that was initially destroyed was successful on subsequent nesting attempts.

At least part of the predation is thought to have been accomplished by resident birds on patrol. In 1972, most of the visiting gulls rested on the south gravel ridge, at least 150 m from the east Glaucous Gull nest. They may have contributed to some of the predation between the territories of the nesting gulls. Resident gulls seemed to concentrate most heavily on the eider depressions that were outside their territories. Although strongly attracted to eider nests close to their own nests, gulls were unsuccessful at these sites once the ducks began to "sit tight" on the eggs. The south shore was regularly patrolled from 150 m west of the east gull nest to within 180 m of the west nest. On the north shore, the patrolled zone began 150 m east of the west nest and terminated within 160 m of the east nest. The existence of these zones suggests that the gulls were observing the territorial boundaries of nesting gulls. However, even the resident gulls seemed to follow this pattern of patrolling.

Figure 9. Egg Island, Alaska, showing the location and utilization of all new sites created during 1972.



The non-incubating member of a nesting pair of gulls left the territory to hunt. When it re-entered the territory, a brief ritual was performed and the birds changed places. On several occasions, a gull patrolled within 150 m of its nest, only to be pursued by its mate until it performed the ritual display and took over incubation duties.

Direct observation of gull behavior at regularly patrolled sites provided evidence that female eiders were well camouflaged. Although gulls seemed to know the location of sites utilized by eiders, they were apparently unable to see the bird unless it moved. Gull behavior at several unoccupied, pre-incubation nests demonstrated their reluctance to approach to within 0.5 m. They approached the nest in a series of advances and backward-hop retreats, gradually coming to the nest rim. (In a backward-hop, the gull takes a short, quick jump backwards, with its wings partly spread and its bill partly open -- a defensive position). Nest material was pecked, accompanied by a backward-hop. This procedure was followed until either an egg was found, the nest was destroyed, or the eider returned. When an egg was located, the gull either cradled or speared it with the bill. The egg was carried at least 3 meters from the nest before it was eaten. Glaucous Gulls consumed eggs using two basic techniques: swallowing the entire egg or eating only the yolk, albumen, and embryo (Table 10). Gulls were seldom harassed by conspecifics while consuming eggs, which allowed them to choose only the energy-rich portion of the egg. In four (67%) cases where more than one egg was present at a nest, the first eggs were cracked and swallowed. Only the contents of the last egg were eaten, however, not the shell. Were the gull to eat

Table 10. Methods of eider egg consumption by Glaucous Gulls on Egg Island in 1972.

Method of consumption	N	%
Swallowed entire	9	34
Whole	1	4
Cracked	8	30
Not Swallowed	18	66
Contents eaten from shell	16	59
Contents dumped from shell	2	7
Total	27	100

each egg slowly, it might attract other gulls to the nest and lose possession of the remaining eggs. It would also risk the return of the female eider. The removal of eggs to a distance of at least 3 m from the nest may be an adaptation to assure that the gull will not be harassed by the eider, should she soon return to the nest.

Incubation

In 1972, the incubation period of the Pacific Eider was 26 ± 1 days (range: 21-28 days, N = 11). This agrees generally with the findings of Milne (1963), Belopol'skiĭ (1961), and Dement'ev et al. (1967) for the European Eider and Guignion (1967) and Choate (1966) for the American Eider. A 28-day incubation period has been suggested by Kortright (1943), Gross (1938), Gudmundsson (1932), and Cooch (1965). Some variation in the incubation period is to be expected, for it is difficult to determine when it begins and terminates. Incubation may begin after the deposition of the first egg (Cooch 1965), but occurs more commonly after three or four eggs have been laid (Cooch 1965; Dement'ev et al. 1967; Milne 1963). Robertson (1929), Belopol'skiĭ (1961), and Guignion (1967) reported incubation to commence following the deposition of the last egg. In sharp contrast to these eiders, most waterfowl species delay incubation until after the laying of the last egg (Bent 1962a; Mendall 1958; Barry 1960; Erskine 1972). It is generally accepted that Common Eiders deposit one egg per day until the clutch is completed (Cooch 1965; Guignion 1967; Milne 1963), although this interval may decline to 15 hours late in laying (Dement'ev et al. 1967). Dement'ev et al. (1967) believed the last 12 hours to 2 days of incubation to be occupied by pipping. Belopol'skiĭ

(1961) has suggested that the length of incubation varies directly with clutch size, with the smaller clutches having a shorter incubation period. Regression analysis of clutch size versus incubation period in my study failed to establish a significant relationship ($F = 5.26$, $P > 0.5$, $N = 7$), although this trend was apparent (Fig. 10). Corresponding to this was a trend towards a shorter incubation period ($t = 1.88$, $0.005 < P < 0.1$, $N = 11$) for nests initiated during the second half of the season (Fig. 11).

In the present study, incubation was considered to begin when the female remained on the nest continuously and to end 1 day prior to her departure with the young. Based upon observations at one nest, incubation began with the deposition of the third egg (assuming a laying rate of one egg per day). The deposition of down may coincide with the onset of incubation. Based upon observations at one nest, down deposition and incubation both began following the laying of the last egg of a three-egg clutch. Cooch (1965) reported considerable variability with respect to down deposition. Some birds added down to their nests after the laying of the first egg, while others deposited no down until the clutch was complete. Once incubation began, the female left the nest infrequently and then only for a short period. In nine absences of known duration, the nest was vacated for 10 ± 5 min (range: 1-25 min). During these absences, females swam, preened, and drank at distances varying from 10 m to perhaps 200 m from the nest. Gull predation could have easily occurred but was never noted. The females were never observed to feed at these times. These findings are consistent with other subspecies (Belopol'skiĭ 1961; McKinney 1965; Cooch 1965; Guignion 1967). In the Pacific Eider, as in

Figure 10. Regression of incubation duration versus clutch size of Pacific Eider nests on Egg Island in 1972.

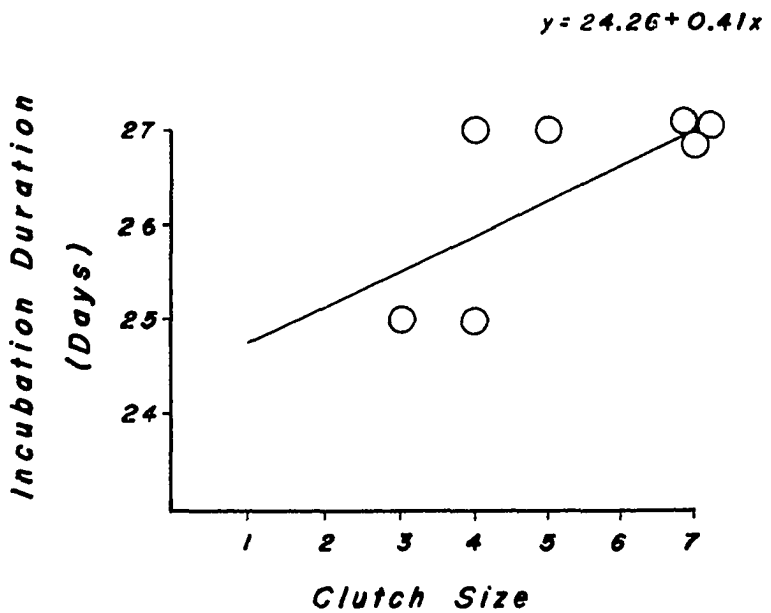
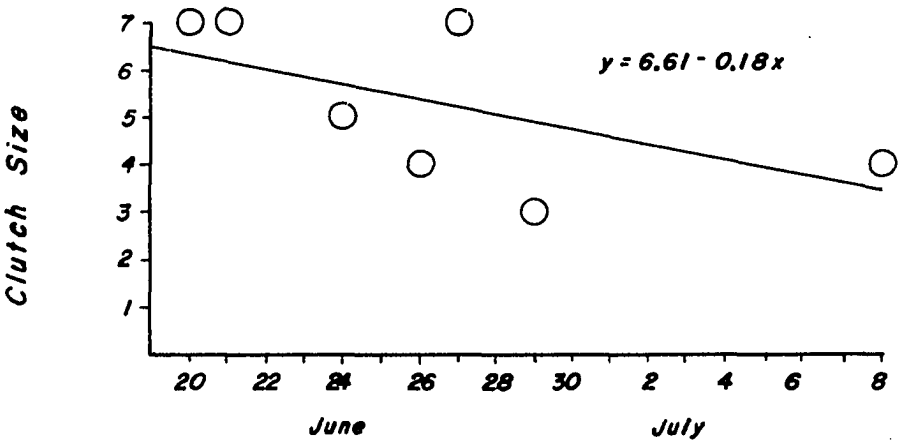
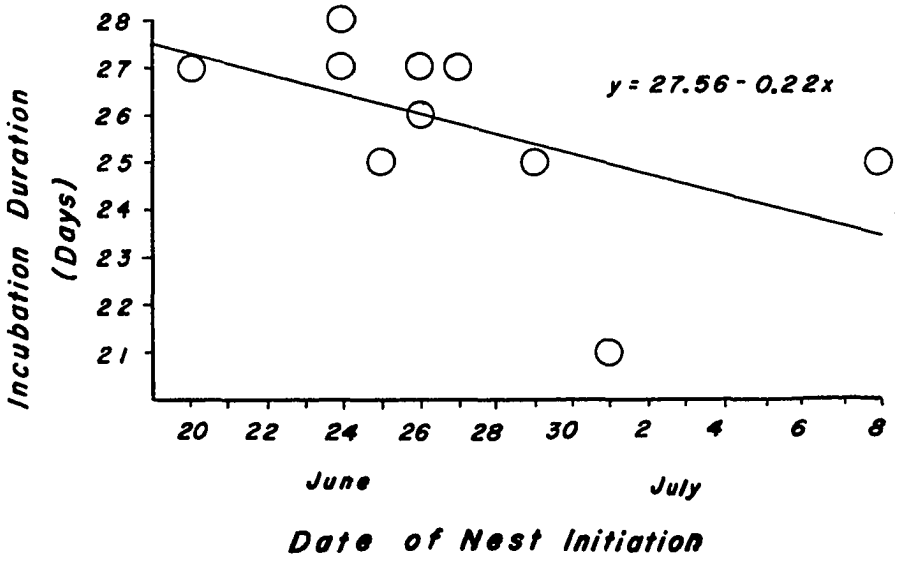


Figure 11. Regression of clutch size versus date of nest initiation and incubation duration versus date of nest initiation of Pacific Eider nests on Egg Island in 1972.





other subspecies, the female always covers the eggs before departing. Absences from the nest were noted at all times of the day. Robertson (1929) recorded a similar behavior in the European Eider.

In general, incubating female eiders are extremely quiescent. They tolerate visiting non-nesting females to within short distances, allowing them to sit within a few decimeters of the nest. Only when these visiting females begin to nibble at the nest materials do the incubating birds show even mild aggression. Incubating eiders allow gulls to approach within a meter before displaying any aggressive behavior towards them. When a gull approaches close to the nest, the eider lashes out with its head, snapping its bill. The gull usually walks around the bird and tries to approach the nest from behind the eider, who meanwhile shifts position on the nest to maintain visual contact with the predator. If the gull approaches within about 0.5 m of the nest, the eider may actually attack it. Five such instances were recorded. As the eider attacks, the gull turns to fly, exposing its back to the duck. This area is clasped by the eider, who holds the screaming, flapping gull for as long as 6 seconds before releasing it and rushing back to the nest. Although gulls sometimes hunted in pairs, they were never observed to use teamwork to rob a nest of eggs, i.e., one gull did not decoy the eider from the nest while the other stole an egg. In two instances, an eider attacked one of two gulls standing at opposite ends of her nest. In both cases, the other gull showed no apparent interest in the eggs.

When frightened from their nests, incubating eiders eject a foul-smelling excreta. This has been noted by others (Cooch 1965; Guignion

1967). Beetz (1916) and Gudmundsson (1932) suggested this to be an adaptation to deter predation. In laboratory experimentation, Swennon (1968) demonstrated the unpalatability of this material to rats and ferrets. It is believed that the long fast of incubating eiders may lead to an internal storage of wastes, with a subsequent increase in the bacterial production of compounds such as indole and skatole (Kear 1963). In the Pacific Eider, the expulsion of this excreta may be an adaptation that deters predation by foxes. I have no observations of Glaucous Gull reactions to fouled eggs.

Nesting Density

The combined nesting density of Pacific and King Eiders on Egg Island was 6 nests per ha (range: 5-7 nests per ha) (Table 2). Egg Island had the highest concentration of nesting eiders of any of the four barrier islands examined in the Prudhoe Bay area. Two islands had no nesting eiders and the third, Stump Island, had an estimated minimum density of 1 nest per ha in 1972. In studies of other subspecies, densities ranged from 7 (Milne 1963) to 3000 nests per ha (Ahlen and Andersson 1970). Guignion (1967) reported a maximum of 221 nests per ha and Choate (1966) reported a range of 67 to 157 nests per ha. My study indicates that Pacific Eiders, at least on Egg Island, nest in lower concentrations than other subspecies.

Clutch Size

Clutch sizes were determined for incubated nests on Egg Island and Stump Island. The overall mean clutch size was 5 ± 1 eggs. Although no significant differences were found either temporally or spatially, some

trends seem to exist (Table 11 and Fig. 10). In 1971, an early breeding season, clutch sizes appear to have been larger than in 1972, a late year. During both seasons, early-nesting birds seem to have larger clutches than those nesting later. In 1972, Stump Island clutch sizes tended to be smaller than those on Egg Island, which became ice-free earlier than the former. In general, it appears that the early-nesters have the largest clutch sizes. Corresponding to this is the trend towards larger clutches during early seasons. My findings on the mean clutch size of the Pacific Eider are similar to those reported by Dement'ev et al. (1967), but somewhat larger than those of Kenyon (1961). The seasonal decline in clutch size appears to be a common phenomenon among bird species. It has been noted in passerines (Perrins 1965; Snow 1958), penguins (Richdale 1957), and various waterfowl species, including the Common Eider (Bellrose et al. 1964; Cooch 1965; Dane 1966; Guignion 1967; Stotts and Davis 1960; Morse et al. 1969). Koskimies (1957a) has suggested that clutch size is genetically controlled, as is the date of laying. Early-nesters are those individuals producing large clutches, while birds which lay smaller clutches nest last. This results in the synchronous hatching of all nests, supposedly at an opportune time for obtaining food for the young. In harsh climates, food resources may be temporally limited and this synchrony might be crucial to the survival of the young (Koskimies 1957a). Others feel that the seasonal decline may be related, at least partially, to the age of the laying bird. Younger individuals nest later (Brakhage 1965; Gates 1962) and lay smaller clutches (Morse et al. 1969; Perrins 1965; Snow 1958) than older birds. This may be due to a lack of experience in the younger females (Brakhage

Table 11. Clutch sizes of Pacific Eiders on Egg and Stump islands.

Nest location and year	N	Clutch size $\bar{X}$ ± 95% C.L.	Range
Egg Island			
1971	10	5.6 ± 1.2	2-8
1972	7	5.3 ± 1.3	3-7
Stump Island			
1972	7	4.6 ± 2.0	1-8
Total			
1971	10	5.6 ± 1.2	2-8
1972	14	4.9 ± 1.1	1-8

1965; Richdale 1957) or physiological differences (Wood 1965). In late seasons, some birds may be physiologically out of laying condition before nesting habitat is available (Barry 1960). Only the late-nesters are able to reproduce in these years and they lay smaller clutches (Barry 1960; H. Milne, personal communication). Thus, those areas which become available later in the season should have fewer nests and smaller clutch sizes than equally suitable localities that are available earlier. This may explain the nesting density and clutch size differences between Egg and Stump islands. Renesting may account for at least part of the smaller clutch sizes. Since it occurs after the initial loss of a clutch, re-nesting is a late-season phenomenon. These nests generally contain fewer eggs than the initial breeding attempt (Gates 1962). Despite the brevity of the arctic breeding season, it appears that the Common Eider is able to renest if predation occurs soon after incubation begins (Turner 1886; Cooch 1965). Dement'ev et al. (1967) reported that follicle scars in the ovary indicated that eggs were produced two or three times per season. Finally, Milne (1963) suggested that increased predation during the latter part of the nesting season may lead to smaller clutches.

Nest Termination

The mean nest termination date in 1972 was 25 July ± 2 days. The first broods departed from Egg Island on 20 July; the last brood left on 4 August (Fig. 4). Essentially all incubated eider nests that year were successful. (One nest, however, was incubated for 4 days, then deserted.) Girard's (1939) method of membrane separation for the determination of nest fate could be used shortly following the vacation of a nest. Within

a few hours to several days, however, eggshells and down were either blown away or carried away by gulls. This phenomenon makes it virtually impossible to determine either the number of nesting attempts or the percentage that are successful on islands that are visited after hatching has occurred. In sharp contrast, Choate (1966) reported that the fate of American Eider nests could be accurately determined up to 6 weeks following the hatch.

The 1972 hatching period was significantly later than that of 1971 ($t = 4.06$, $P < 0.001$, $N = 25$). The mean hatching date in 1971 was 19 July ± 2 days, whereas in 1972 it was 25 July ± 2 days, a difference of about 6 days. Similar delays were reported in the Prudhoe Bay area that year for insects (about 10 days) (S. F. MacLean, personal communication) and inland-nesting waterfowl (about 8 days) (R. Bergman, personal communication).

As the eggs begin to hatch, the incubating female became more alert and active at the site. She shifted positions and arranged the nest more frequently. She gave soft, chuckling vocalizations, unlike those during nest searching. This restlessness at hatching was also noted by Milne (1963).

Seven instances of nest termination were observed. Of these, five (71%) were terminated while no non-nesting female eiders were in attendance at the nest. Female eiders were present at the remaining two nests at termination. The general behavior pattern at termination was the same, regardless of the presence or absence of other eiders: the female led the brood to the nearest water fairly rapidly. When other eiders were present, the broody female tolerated them to within a meter of herself

and her brood. All who ventured nearer were attacked and driven away. King Eiders were attacked most intensely. Upon reaching water (usually the Gwydyr Bay), the female immediately bathed, followed by wing flapping. She and her brood remained in the shallows near the island, where the female (and perhaps the young) fed. The female cruised along the wind-protected shore with her head and neck submerged, apparently feeding along the bottom. The young followed her and were thought to eat food items she dislodged from the bottom. They may have been feeding upon young isopods, Mesidotea entomon. Several female isopods of this species with well developed young in their marsupia were found in the quiet shallows near the base camp in late July 1972. Pethon (1967) found amphipods and isopods to be the most important food of young eiders. Milne (1963) and Choate (1966) noted that young broods tend to feed in sheltered, shallow areas.

Dense fog during the hatching period interfered with observations of the broods. I was able to follow the movements and activities of only three broods. In two instances, they remained in association with barrier islands until my visual contact with them was lost. The third brood crossed the island and swam out to sea. At this time, the Beaufort Sea ice pack was hard-pressed against the north shore. The female therefore had to lead the young around and over the ice.

The broods were not harassed by gulls while en route to water, despite the fact that they sometimes passed within 3 meters of the predators. This phenomenon was also observed in the American Eider (Guignion 1967) and other island-nesting waterfowl (Dwernychuk and Boag 1972; Vermeer 1970). No gull harassment was noted even after the young reached water.

This agrees with Choate's (1966) observations but contrasts strongly with Dwernychuk and Boag (1972) and Vermeer (1970), who reported heavy predation by California Gulls (Larus californicus) soon after the broods entered water. Mortality factors in young Pacific Eiders are not known. However, it appears that Glaucous Gulls have little effect on them after they leave the nest.

The non-nesting female eiders attendant at nests were also seen in association with females and their young. These "aunts" (Robertson 1929) are thought to be failed breeders or immatures (Guignion 1967; Milne 1963). In the present study, these birds appeared to be present from 4 July until the end of the field season. This contrasts with Guignion (1967) and Milne (1963), who first noted the "aunts" during the hatching period. Behaviorally, these birds could be distinguished from potential nesters on Egg Island by several factors. Although they occasionally actively searched for nest sites, they did not remain in the depression while investigating it as did potentially nesting birds. Instead, they crawled from the site to gather sticks and did not return to it. They were never aggressive towards nesting eiders, although they frequently visited them. Instead of moving quickly from one potential nest site to another, as did the breeders, these birds often remained asleep near a depression for several hours. When investigating a site, they never showed any intense agonism towards visiting eiders. They made new scrapes until the end of the field season.

The sighting of two females attending a group of eight young near Egg Island in 1972 provides some evidence that creching may occur in the Pacific Eider. This behavior has been studied in the European Eider

(Gorman and Milne 1972). Milne (1963) suggested that creching may not occur when eiders are sparse and little brood contact occurs.

Two instances of aberrant behavior in broody females were noted. In each case, the broody female approached and attacked an incubating eider. In one of these instances, the attack was successful and the incubating bird was temporarily dislodged from its nest. During this interval the displaced bird tried futilely to regain possession of its nest. The visiting female meanwhile brooded its young on top of the eggs of the dislodged nester. After 2 hours, the broody female departed with its brood and the incubating bird returned to the nest and resumed incubation. This may indicate that the incubation drive was not fully satisfied by the successful hatching of the brood.

Nesting Success

In 1972, 33% of Pacific and King eider nesting attempts were successful and 58% of the eggs hatched (Table 9). An average of 1.5 young were produced per nesting attempt. This is similar to the 39% and 36% nest success reported by Choate (1966), 29% by Paynter (1951), 30% by Gershman et al. (1964), and 29% and 32% in two of Guignion's study islands (1967). It is considerably lower than Milne's (1963) 68% and Guignion's (1967) 52% success.

The hatching success found on Egg Island was higher than the 39% found by Choate (1966) and the 13% and 29% on two of Guignion's other study islands (1967). It was lower than the 95% success reported by Milne (1963).

My figure on the production of young per nesting attempt falls well

within the range reported by both Choate (1966) and Guignion (1967). They found 0.9 to 3.0 and 0.4 to 2.0 young per attempt, respectively.

King Eiders

King Eider pairs also investigated Egg Island depressions for potential nest sites. However, their overall breeding success was considerably lower than that of the Pacific Eider. Comparing the ratio of the total investigating pairs to total initiated nests in both the Pacific and King eiders, it was found that the latter species attempted significantly fewer nests ($\underline{X}^2 = 5.87$, $0.01 < \underline{P} < 0.025$, $N = 42$) than the Pacific Eiders. The success of these attempts, however, was comparable (33%, $N = 3$) to the Pacific Eider (33%, $N = 39$).

The dearth of nesting attempts by King Eiders is probably due to interspecific competition for nest sites, as suggested by Larson (1960) for island-nesting King and Common eiders. Both species apparently have similar nest selection criteria, as evidenced by their nest searching efforts. However, nest searching King Eiders always lost possession of a depression to Pacific Eiders during interactions at investigated sites. Pacific Eiders frequently followed a nest searching pair of King Eiders, driving them from successive sites. Pacific Eiders were believed to be socially dominant over the smaller King Eiders. During most interspecific interactions, the King Eiders retreated at the approach of the Pacific Eiders. In a few instances, combat was observed. Only when a King Eider was "sitting tight" on a nest was it successful in defending the site. Nest initiation in this species was delayed until after 90% of the Pacific Eider attempts had been made. King Eider nesting inshore

began on 19 June (R. Bergman, personal communication), while no attempts offshore were noted until 4 July. The nesting attempts by King Eiders on Egg Island may represent renests (following an inshore failure), different year-class birds, or simply late nesters.

General Discussion and Conclusions

Reproduction is energetically costly and potentially dangerous to the nesting bird, who is tied to the nest during incubation. Strategies which provide protection for the incubating bird and which maximize the number of surviving young are important considerations in delineating the basic breeding biology of a species. The present study of the Pacific Eider concentrated mainly upon the behavioral components, including both inter- and intraspecific considerations, of their breeding biology.

It appears that these eiders have developed a fairly successful system to overcome the hazards inherent in reproduction, the most important of which is predation. On the North Slope of Alaska, eiders face potential predation from Arctic Foxes, Glaucous Gulls, and jaegers.

Larson (1960) reported that the mere presence of Arctic Foxes on the eider breeding grounds will inhibit their nesting attempts. He suggested that the breeding of eiders on offshore islands is due to the more common occurrence of foxes on the mainland. In my study, no foxes were ever observed on the island during the breeding season. Although it is possible for them to be rafted to the barrier islands during the summer, the discontinuous nature of the ice makes this unlikely. Eiders also appear to postpone nesting attempts until the islands are ice-free and thus inaccessible to the foxes. The timing of break-up in the Gwydyr

Bay is apparently dependent upon both the overflow of the nearby river and subsequent rise in temperature. Although overflow dates were essentially the same for both 1971 and 1972 (R. Bergman, personal communication), lower temperatures shortly thereafter in 1972 retarded the melting process (S. F. MacLean, personal communication) and postponed the arrival of breeding eiders on Egg Island. This occurred despite the fact that the island was essentially snow-free prior to break-up.

Pacific Eiders have also apparently adapted to the avian predators that frequent these islands. Unlike the foxes, these predators threaten only the eggs, not the nesting bird. By nesting within the territory of the resident gull, the eiders may receive protection from other gulls and jaegers. Eiders have therefore effectively reduced the number of potential predators of their nests. In addition, Glaucous Gulls appear to have developed a social system which inhibits intensive predatory activities within their own territories. It appears that gulls penetrating the territory on foot are chased by the incubating bird, unless they perform a ritual recognition display. This is followed by nest relief of the incubating member of the pair. If the display is not given, the intruding bird is driven from the territory. Unfortunately, these conclusions are based upon only a few general observations. The intraspecific interactions of these gulls on their territories need to be examined in detail and clarified.

Eiders seem to prefer nest sites that offer camouflage, a visual barrier to predators, and some physical protection from the prevailing northeast wind. The bright-colored males spend only a short time at the nest site during the initiation stage. Thus, they do not attract predators

to the nest. In the case of early nesters, the maintenance of the pair bond and territorial behavior suggests that renesting may be possible in this species. Renesting had been suspected in other subspecies and is thought to be more likely if the nest is destroyed during early incubation (Guignion 1967; Milne 1963). The abbreviated period of nesting in the Pacific Eider may account for the short period of potential renesting. It would thus seem advantageous to nest early, while renesting is still possible. There is also a difference in the year-class of nests used early and late in the season. Depressions remaining from the preceding year are utilized first. Gulls seem to learn quickly the location of these sites and examine them regularly. By this time, however, the eiders have switched to the utilization of newly created sites. The ultimate reason for this shift is not known. It may be related to gull predation patterns or to the moisture regimes of the areas containing old and new sites. The former sites are located generally higher on the island and would become dry early in the season. New sites are located on the periphery of the island and become dry later. Many of these sites are destroyed annually by fall storms, after the breeding season. This allows for the construction of new sites in this area each year, without increasing the number of depressions over successive years.

Although the 33% nest success on Egg Island appears to indicate heavy gull predation, the 58% egg success may be a more realistic estimate of nest destruction. After the loss of an incomplete clutch, it is quite possible that the female continued her nesting efforts at either the same nest or another. This is not really renesting, but rather a continuation of a single clutch of eggs. Thus, although gulls may depress the number

of eggs in the nest, their effect on eider production may not be as great as indicated by the low nesting success.

Over 70% of all egg losses to predators occurred during an absence of the female during the nest initiation stage. Only one instance of gull-induced desertion was recorded. Behavioral observations of interactions between eiders and gulls indicate that eiders are quite capable of defending their nests. It is apparent that the eggs are most vulnerable to predation during the early stages of nest initiation. At this time, the eggs are deposited in the nest and left unattended by the female for an estimated 48 hours before incubation begins. Once the female begins to "sit tight" on the eggs, the possibility of predation is almost non-existent. In this study, the continuous attendance of a female on a nest has been equated with incubation. This is not necessarily true and should be explored. If a female could attend the nest without incubating, the nest would be exposed to predators for a lesser amount of time. This would definitely be advantageous. Norton (1972) found sporadic incubation to occur during laying in Baird's Sandpipers (Calidris bairdii). He postulated this to represent a balance between the danger of allowing the eggs to freeze and the danger of inducing asynchrony by allowing too much development in the first-laid eggs. In the Pacific Eider, it appears that incubation may begin before the clutch is complete. Other waterfowl usually initiate incubation after the completion of the clutch. It is possible that the present clutch size represents a compromise between the number of days the nest can be left unguarded and the number of eggs that can be laid after incubation begins and still maintain good hatching synchrony. This has recently been suggested by Johnsgard (1973). The

shortening of the egg deposition interval late in laying (Dement'ev et al. 1967) may be an adaptation to promote synchrony. Brood parasitism may effectively shorten the pre-incubation period by reducing the overall laying interval at a nest. Since the stage of laying at the onset of incubation was not determined, it is possible that brood parasitism led to rapidly completed clutches. In this case, incubation beginning 2 or 3 days following nest initiation may coincide with a full clutch of eggs. Brood parasitism is a fairly common phenomenon among waterfowl (Weller 1959). Intraspecific parasitism was noted in semi-colonial King Eiders (Hansen et al. 1956). Dau (1974) has recorded parasitism in the Spectacled Eider (Somateria fischeri). It has also been described in the Common Eider (Gross 1938; Dement'ev et al. 1967; Guignion 1967). Parasitism may be more prevalent in younger birds (Weller 1959) and in high density nesting areas (Vermeer 1968).

Although the nest site criteria of Glaucous Gulls and Pacific Eiders seem to overlap, active competition for sites is apparently non-existent. Gulls nest before the eiders arrive on the island. My data show that King Eiders, however, actively compete with Pacific Eiders for the same sites. King Eiders are almost entirely excluded from breeding on Egg Island by the larger, more aggressive Pacific Eiders. Only one King Eider nesting attempt was successful over the 3 years of nesting records for the island.

Many questions remain unanswered. In this study, the gull-eider association appears to provide some benefit for the waterfowl, as well as the gulls. However, the development of this association is still unclear. It is not known whether the eiders are drawn to the island by

the presence of nesting gulls or in spite of them. The role of "aunts" in the colony and their behavior needs clarification. They may contribute to the overall nesting success through brood parasitism. We need to know whether these are failed breeders, immatures, or both. Their amicable association with incubating birds and their construction of scrapes late in the season may be an important learning exercise for future nesting attempts (Lack 1968).

APPENDIX A.

OTHER NESTING BIRDS

In addition to Pacific and King eiders, Black Brant, Glaucous Gulls, and Arctic Terns nested on Egg Island. Of these three additional species, the gulls and terns apparently nest in equal numbers each year, while only one brant nest was found during the three breeding seasons.

The brant nest (Fig. 6) occupied the Elymus site during 1971. It was the first waterfowl nest to hatch. I therefore assume the brant had established their territory before the eiders began to initiate nests. Behaviorally, the brant were clearly dominant over non-nesting female eiders. I was unable to observe interactions between brant and nest-searching eiders.

Glaucous Gulls nested on Egg Island all 3 years. Their nests were generally constructed on gravel ridges and were composed of an elevated mound of dried grass roots, which were gathered from the drift debris on the island. There were nine nests in 1971, three in 1972, and at least three in 1973 (R. Bergman, personal communication). In 1972, gulls were present on the island at the time of my arrival, 20 May. Courtship behavior was not observed until the overflow water from the Kuparuk River reached the island on 2 June. Copulation was also recorded at this time. Nest building was first noted on 10 June. Egg laying was estimated to have occurred between 15 and 20 June. By 18 June, incubation had begun

at one nest. Hatching was completed by 17 July. Two of the three nests were successful. The third nest was deserted during the laying stage. The unsuccessful pair remained on Egg Island throughout the summer. Courtship behavior in this pair was noted as late as 26 June. Each of the two successful nests hatched three young. It is thought that the chicks were fed mainly isopods, Mesidotea entomon.

Like the gulls, Arctic Terns nested on Egg Island all three seasons. There were approximately five nesting pairs in 1971, five in 1972, and at least three in 1973 (R. Bergman, personal communication). In 1972, the terns arrived in the Egg Island area on 3 June. Courtship was first noted on 8 June and lasted until 9 July. Copulation was first recorded on 9 June and was last noted on 8 July. Five nests were initiated between 22 June and 3 July. Only the last nesting attempt was successful. The others were terminated early in incubation. The successful nest terminated on 22 July with the hatching of both eggs. Both chicks were found dead, near their nest, on 27 July. Dense fog may have severely hampered the feeding attempts of the adults. Thus, the young terns may have starved.

APPENDIX B.

MANAGEMENT RECOMMENDATIONS

While on the breeding grounds, Pacific Eiders face potential disturbances from mammalian and avian predators. As previously discussed, the eiders have an effective system to avoid predation from Arctic Foxes, gulls, and jaegers. With impending oil development, however, eiders are seriously threatened by the potential loss of breeding habitat to oil drilling and the possibility of high mortality in oil spills along their coastal migration route.

During the arrival, nest searching, and laying stages, from mid-June through mid-July (Fig. 4), Pacific Eiders can be easily frightened from their nesting islands by the mere presence of humans. Low-flying aircraft (altitudes less than 100 m at distances up to 2 km) can also disturb the birds during this period. Pacific and King eiders and Old-squaws are apparently more sensitive to helicopters than to small planes. Once an eider has established a nest and has begun incubation, it becomes increasingly difficult to frighten her from the island. The sensitivity of incubating females to human presence and noise seems to decrease steadily through incubation until the eggs begin to pip. A helicopter visit during the searching and early nest initiation stage frightened all birds from the island. In contrast, a helicopter which landed on Egg Island during the late incubation period failed to frighten any incubating female from its nest. After pipping begins, an

eider's sensitivity increases sharply. A female Pacific eider late in incubation may be easily approached to within 7 m before she shows any willingness to flush. During pipping, however, the same bird may unexpectedly flush at 10 m. If a female flushes and is accompanied by a single young, she will depart from the island with that duckling and leave the remaining eggs and young behind. This information was obtained by human presence on Egg Island. No low overflights were noted during the hatching of a nest. The hatching period lasts from mid-July through early August.

Low overflights may cause temporary disturbances to the eiders, but this is not as serious a threat to breeding eiders as is the presence of humans on the offshore islands. Recreational boating disturbances along the north coast of Alaska are not so common as on the St. Lawrence estuary (Guignion 1966) or in Maine (Choate 1966). The possible use of barrier islands for oil drilling does, however, pose a serious threat to breeding eiders. Offshore wells should therefore be restricted to islands with low-density populations.

During the spring and summer migrations, Pacific Eiders and other waterfowl remain close to shore, often following the string of barrier islands or the coastline. In addition, the lagoon areas are utilized by molting Oldsquaws and broods of eiders. A mid-summer spill, coupled with a period of inshore movement of ice, could easily force the birds into a very narrow band of open water near the coast. Under such circumstances, the birds could be quite susceptible to oil spills. Even a small spill could affect a very large number of birds.

If offshore oil development must take place on the Beaufort Sea coast, it should be limited to areas that: (1) have small breeding

populations of birds, (2) would permit easy control of spills, and (3) are located away from rivers and river deltas. Deltas are the first open-water areas in the spring and attract large concentrations of migrating waterfowl. The rapid movement of overflow in these areas would impede the control of a spill. The cessation of offshore drilling from mid-May through mid-September would minimize the possibility of oil spills during the short time that avifauna utilize the area.

If caution is not exercised in the exploration and development of oil resources along the Beaufort Sea coast, it is quite possible that several species of birds could be eradicated from that area with a single, relatively small oil spill.

APPENDIX C.

SUGGESTIONS FOR FURTHER STUDY

1. Gull-waterfowl associations form a fascinating study. Waterfowl receive some protection from resident gulls, but also lose either eggs or young, or both, to them. Yet these associations persist. Their development is still unclear. Are the waterfowl drawn to the gulls? Or do the gulls nest in established waterfowl colonies, taking advantage of site tenacity in waterfowl? Or are both species drawn independently to the islands by similar nest selection criteria?

2. In the present study, gulls appeared to hunt for eider nests mainly outside their territories. My limited observations of gull displays at the nest suggest that the returning member of a pair is forced from the territory if a mutual recognition display is not performed. This display is followed by an exchange of duties. If this is the usual behavioral pattern, then eiders nesting within a gull's territory should receive additional protection. The intraspecific interactions of gulls on their territories need to be examined in detail and related to the site selection criteria of waterfowl.

3. Eider nests tended to be located at successively lower elevations over time. I have hypothesized that this may be related to different moisture regimes of these sites as the snow melts and the island dries. However, I have no quantitative data to substantiate this.

4. Based upon a comparison of nesting densities and clutch sizes

of Pacific Eiders on Egg and Stump islands, I feel that the islands which become ice-free earliest should support the highest concentrations of nesting eiders. Such islands should be located in the river deltas. This intensive nature of my study precluded extensive nest searching efforts, except in the immediate vicinity of Egg Island. Other islands should be examined to test this hypothesis.

5. For a long-term behavior study, banding would be essential. The use of this technique would aid immensely in determining the nature and extent of such supposed age-related phenomena as (1) the occurrence of "aunts" in the breeding colony, (2) brood parasitism, and (3) age-specific productivity and its seasonal timing.

6. Koskimies (1957a) has suggested that the timing of hatch may be related to the seasonal abundance of food resources for the young. There appeared to be an abundance of young isopods during the end of the hatching period. The relation of food resources to the timing of hatch needs much more study.

7. It is not difficult to follow the breeding cycle of the Pacific Eider from their arrival through the hatching period, if the observer is provided with a good observation blind. However, the post-hatching mortality factors are still unknown. Mendenhall (personal communication) is examining this in the European Eider in Scotland. This should be studied in the Pacific Eider as well. Duckling mortality studies along the Beaufort Sea coast pose a difficult problem, due to the breeding densities and the apparent dispersion of broods.

APPENDIX D. Location and fate of Pacific and King eider nests on Egg Island in 1972.

Nest	Location of nest							
	North[a]		Center		South[a]		Total	
Category	N	%	N	%	N	%	N	%
Successful	3	23	7[b]	41	4	36	14	34
Unsuccessful	10[d]	77	10[c]	59	7	64	27	66
All nests	13	32	17	42	11	26	41	100

[a]Within 15 m of the shore.

[b]Includes one King Eider nest.

[c]Includes one deserted Pacific Eider nest.

[d]Includes two King Eider nests.

APPENDIX E. Location and fate of Pacific and King eider nests in 1971 and 1972.

Nest year, Location, and Fate	Distance from gull nest (m) <50 N	%	>50 <100 N	%	>100 <150 N	%	>150 <200 N	%	>200 <300 N	%	>300 N	%	Total N	%
1972														
South														
Successful	-		8[a]	80	-	-	1	25	1	20	-	-	10	50
Unsuccessful	-		2	20	1	100	3	75	4	80	-	-	10	50
Total	-		10	50	1	5	4	20	5	25	-	-	20	100
North														
Successful	1	50	1	50	1	25	-	0	2[b]	25	-	-	5	26
Unsuccessful	1	50	1	50	3[b]	75	3[b]	100	6	75	-	-	14	74
Total	2	10	2	10	4	21	3	16	8	43	-	-	19	100
1971														
South														
Successful	8		1		-		1		1		1		12	
North														
Successful	4		-		1		-		-		-		5	

[a]Includes one deserted Pacific Eider nest.

[b]Includes one King Eider nest.

APPENDIX F. Fate of Pacific and King eider nests initiated at old and new sites on Egg Island in 1972.

	Nest Fate			
Nest	Successful		Unsuccessful	
Category	North	South	North	South
Old	2	4[a]	9	8
New	3[b]	6	5[c]	2

[a]Includes one deserted Pacific Eider nest.

[b]Includes one King Eider nest.

[c]Includes two King Eider nests.

APPENDIX G. Fate of Pacific and King eider nests initiated in various cover types in 1972.

Nest	Cover type[a]									
	Gull nest		Gravel ridge		Sticks, logs		Honckenya		Elymus	
Category	N	%	N	%	N	%	N	%	N	%
Successful	3[b]	60	9	47	10[c]	46	0	0	2	67
Unsuccessful	2	40	10	53	12[d]	54	4	100	1	33
All nests	5	9	19	36	22	41	4	8	3	6

[a]A single nest may be associated with more than one cover type.

[b]Includes one deserted Pacific Eider nest.

[c]Includes one King Eider nest.

[d]Includes two King Eider nests.

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